EARLY MIGRATORY BEHAVIOR OF NORTHERN FUR SEAL (*Callorhinus ursinus*) PUPS FROM BERING ISLAND, RUSSIA

A Dissertation

by

OLIVIA ASTILLERO LEE

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

May 2011

Major Subject: Wildlife and Fisheries Sciences

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Approved by:

Chair of Committee,	Randall W. Davis
Committee Members,	Douglas Biggs
	Frances Gelwick
	Bernd Würsig
Head of Department,	Thomas E. Lacher

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ABSTRACT

Early Migratory Behavior of Northern Fur Seal (*Callorhinus ursinus*) Pups from Bering Island, Russia. (May 2011)

Olivia Astillero Lee, B.A., University of Hawaii at Hilo

Chair of Advisory Committee: Dr. Randall Davis

I examined the population trends of northern fur seals (*Callorhinus ursinus*) using an age-specific metapopulation model that allowed migration between rookeries. Mortality and birth rates were modified to simulate future population trends. I also examined the early migratory behavior and habitat associations of pups from Bering Island (BI), Russia. I instrumented 35 pups with Mk10-AL satellite tags and stomach temperature telemeters which provided diving, foraging and location data. I hypothesized that some aspects of pup behavior from the stable BI population differed from the behavior of pups from the unstable Pribilof Islands (PI).

The population model revealed that emigration did not contribute significantly to the current PI population decline. However, large source populations contributed significantly to population growth in newly colonized rookeries. A stabilization of the PI population was predicted with a 10 to 20 % reduction in both juvenile and adult female mortality rates.

The diving behavior of pups showed a general progression towards longer and deeper dives as pups aged, particularly between 1600 – 0400 (local time), that was

similar to PI pup behavior. However, unlike pups from the PI, I found three main diving strategies among BI pups: 1) shallow daytime divers (mean depth = 3.56 m), 2) deep daytime divers (mean depth = 6.36 m) and 3) mixed divers (mean depth = 4.81 m).

The foraging behavior of pups showed that most successful ingestion events occurred between 1600 – 0400, with successful ingestion events lasting 25.36 $\pm$ 27.37 min. There was no significant difference among the three strategies in the depth of successful foraging dives. I also examined the foraging search strategies in adult females and pups. Both pups and adults conducted Levy walks, although pups foraged in smaller patches (1 km scales).

Using a logistic model to determine habitat associations, I found that pup locations were positively correlated with increasing chlorophyll a concentrations, distances from shore, and sea surface temperatures, and were negatively correlated with depth. There was no significant relationship between all pup locations and the regions (peripheries or centers) or types (cyclonic or anti-cyclonic) of eddies, but ingestion event locations were related to mesoscale eddy peripheries.

DEDICATION

For mum and dad who let me choose my path.

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This research project would not have been possible without the assistance of the following scientists in the field: Dr. Iain Staniland, Dr. Vladimir Burkanov, Dr. Russell Andrews, Vladimir Vertyankin, and Dr. Randall Davis. All of them made my Russian field work enjoyable and successful. I thank Valentina Burkanov for her assistance with the logistics in Russia, and I thank my Russian hostess on Bering Island who so kindly made my stay more comfortable while waiting for a flight home.

My committee members provided tremendous support and encouragement during the entire doctoral process, including help with the bureaucratic problems faced as an international student, and even shelter when I was displaced by a hurricane. I am grateful to Dr. Douglas Biggs who guided me through the oceanographic processes affecting pups in their migration, Dr. Bernd Wursig showed me how social processes and individual behavior plays a large role in pup development and growth, and Dr. Frances Gelwick introduced me to the challenging world of multivariate statistics and the many facets of ecology. Finally, my advisory chair, Dr. Randall Davis, provided both financial and academic support with both the masters and doctoral projects he chaired. I would have never had such amazing research opportunities if it were not for his guidance and help.

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population model possible, and I thank him for all his encouragement and helpful critiques to improve it. I thank Michael Coyne for his help with the STAT program, and Michael Cameron and Jeremy Sterling from the National Marine Mammal Laboratory for sharing their knowledge. I thank Mary-Anne Lea who shared her findings on the Pribilof Islands pups, and my intern Ashley Fleeger who helped me enormously with the busy work of downloading and organizing data.

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CHAPTER I

INTRODUCTION

The northern fur seal (*Callorhinus ursinus*) is a wide-ranging migratory species (Fig. 1), but because of its historical importance as a commercially hunted species, it is also one of the most studied marine mammals. This species was first described by Georg Wilhelm Steller in 1751 and shortly after the discovery of the two largest breeding populations on the Pribilof and Commander Islands, a long history of human impact on northern fur seal populations ensued (Scheffer et al. 1984). Early hunting practices were indiscriminant of sex and age classes, and it was not until obvious declines in fur seal numbers were observed that the first management plans were put into place (Roppel & Davey 1965, Roppel 1984, Scheffer et al. 1984, Gentry 1998). Temporary hunting moratoriums allowed populations to recover, but the estimates of sustainable harvests were made with little information on northern fur seal biology.

A major problem with early fur seal harvests was that animals ranged in international waters and were hunted by several countries with different management plans. The International North Pacific Fur Seal Treaty of 1911 was a significant step towards northern fur seal management and was one of the earliest examples of a multi-national fisheries management policy (Atkinson 1988). The treaty provided exclusive hunting rights to Russia and the United States, whereas countries without resident fur seal rookeries (including Japan, Britain and Canada) were offered a share of the profits

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This dissertation follows the style of *Marine Ecology Progress Series*.

in exchange for halting their own hunting practices (Gentry 1998). Early management plans had mixed success. Some regulations, including ending pelagic harvests, resulted in visible increases in population growth without long lag periods between the end of harvests and an increase in population size, but other policies were far less successful.

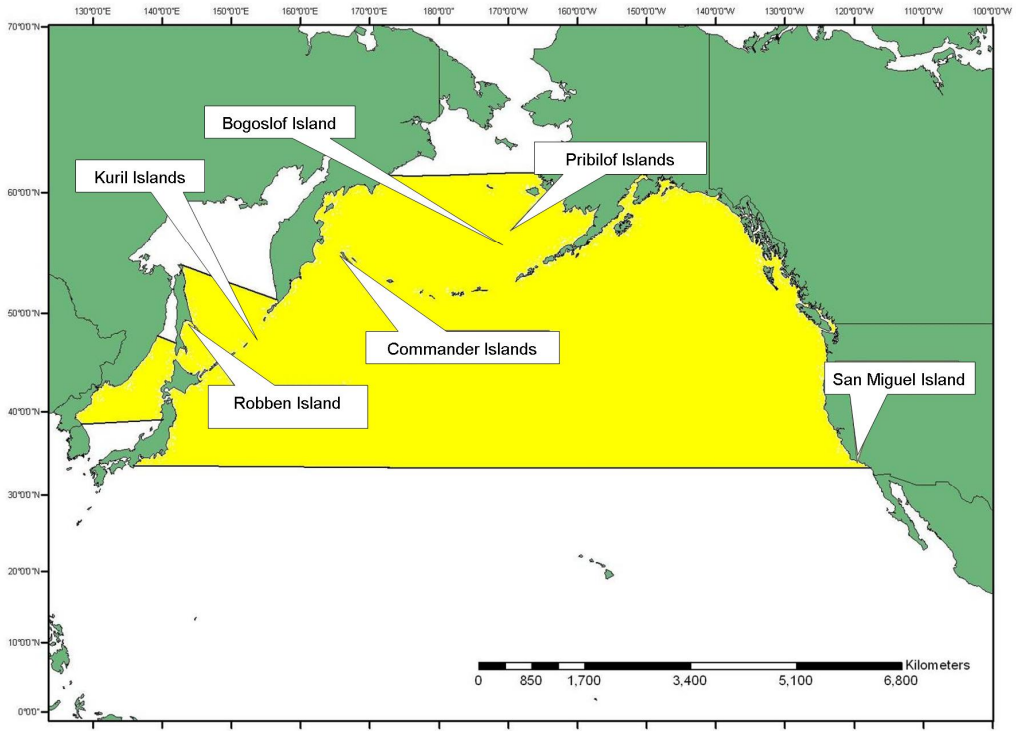

Fig. 1. Northern fur seal breeding populations and species range (yellow).

One of the worst management plans occurred on the Pribilof Islands in the late 1950's. Historically, the largest northern fur seal population has been found on the Pribilof Islands, and it remains so today. Unfortunately, the Pribilof Island population is also showing the most drastic declines despite the fact that commercial harvests ended in 1984.

The current population decline in the Pribilof Islands started when adult females were harvested as part of the Herd Reduction Program. This practice was conducted in response to the lowered juvenile male harvests that occurred in the early 1950's. The Herd Reduction Program decreased herd size by killing over 300,000 females from the Pribilof Islands (Roppel 1984) in an attempt to decrease competition between young of the year and juvenile pups. It was ultimately expected that by reducing intraspecific competition among young of the year and juveniles, the juvenile natural mortality rates would also be reduced, therefore allowing better harvests of juvenile males in the future. Unfortunately, between 1958 – 1968 when this program was in effect (Testa 2005), all sex and age classes declined. Commercial harvests in the Pribilof Islands ended in 1984 amid concerns of the precipitous population declines, but the population is still declining today. In contrast, the second largest fur seal population in the Commander Islands was not subjected to large-scale female harvests, and this population was allowed to grow. The Commander Islands population stabilized in 1960, and it remains fairly stable today.

Mortality Factors

The inability of the Pribilof Island population to recover to its former size after commercial harvests ended prompted more research on other sources of northern fur seal mortality. Simulation models of northern fur seal population trends suggest that increased adult mortality rates were causing the continued, downward population trends (Trites & Larkin 1989, Chapter II). Sources for increasing the adult mortality rate have been suggested and include: entanglement, increased prey competition with fisheries and

increased orca predation. However, quantifying the effects of these factors have been difficult or impossible.

Despite the emphasis that population models place on adult mortality rates, the greatest natural mortality occurs in pups, particularly during their first winter migration (Gentry 1998). Northern fur seal pups are weaned by the age of *ca.* four months and take part in long winter migrations where they encounter unfamiliar habitats and face many survival challenges. Pups may remain at sea for up to two years before returning to shore in summer, making this life stage one of the most difficult periods to study.

Prior to weaning, shore-based studies provide sufficient information on factors affecting pup survival. An increased occurrence of hookworm in very young pups is a cause of some pup mortality (Lyons 2000), but its occurrence on islands with growing northern fur seal populations suggest it may not be serious enough to cause population declines. Other studies suggest that some Pribilof Islands pups suffer from nutritional stress due to poor maternal provisioning, and subsequently, pups are weaned at a much lower mass which may affect their survival at sea (Banks et al. 2006, Iverson et al. 2008).

Changing climate and oceanographic conditions at sea have been known to affect foraging behavior of adult fur seals, and changes in prey abundance and distribution have also been documented. Given the importance of environmental factors on adult fur seal behavior and survival, it is reasonable to assume that naïve pups would be even more affected by changes in climatic conditions during their first winter at sea.

Studies on the migratory behavior of northern fur seal pups have only recently begun since technological advances have allowed individuals to be tracked during their migration. Pups from the Pribilof Islands are now known to range as widely as adults and appear to be as attracted to the same oceanographic features such as eddies. There is an early learning period during which pups refine their hunting skills and display shorter and shallower dives than adults (Baker 2007). The duration of the learning period and locations of preferred foraging habitat may provide important clues about the survival rates of northern fur seal pups at sea. Unfortunately, the emphasis on the migratory behavior of pups has previously involved only individuals from the declining population on the Pribilof Islands and the recently established San Miguel Island, both on the eastern end of the northern fur seal range.

In order to establish whether behavioral differences are adversely affecting pup survival rates in the Pribilof Islands, studies are needed of the pup behavior in the western Pacific, where populations are relatively stable or growing. This study was conducted to provide the first glimpses of pup behavior from the second largest fur seal population in the Commander Islands to determine if behavioral differences occur between pups from the eastern and western Pacific.

Study Site and Animals

The study site was located in the northwest rookery of Bering Island, Russia (*ca*. 55.29°N, 165.77°E). Bering Island is the larger and more western island of the Commander Islands, with the smaller Medny Island also containing northern fur seal

rookeries. The study site was adjacent to a Steller sea lion (*Eumetopias jubatus*) rookery with some space sharing between the two species, but for the most part they remain separated by a rocky cliff that acts as a physical boundary. The 100 m isobath is farther from the coast on the north-western side of Bering Island compared to the eastern side, which has a more abrupt slope. The high latitudes of both the Commander and Pribilof Islands provide similar on-shore climates, but there are major differences in the direction and strength of currents flowing through the channels and passes that border these islands.

The individuals in this study were pups tagged at the end of October 2007 within days to weeks of the time that they were expected to depart their natal rookery for the winter (Gentry 1998). During this time, there were a few adult males still present on the rookery, but mostly adult females remained. In a concurrent study, twelve lactating adult females were instrumented with a tag (either satellite or geolocation), and some results of that study are included in Chapters V and VI. Individual pups weighed at least 14 kg, which is approximately 6% and 28% of an adult male's and female's weight, respectively. The minimum weight limit was chosen as an indicator of individual fitness.

Research Objectives

Pups from the Pribilof and Commander Islands may face similar environmental conditions and degrees of intraspecific competition due to their large population sizes and high latitudes. The research objective of this study was to compare the two populations in order to better understand whether differences in pup behavior could

affect pup survival and subsequently contribute to the decline of the Pribilof Islands population. The primary hypothesis in this study was:

H_0: Movement patterns, habitat preferences and dive behavior are similar for pups from the Commander and the Pribilof Islands.

Several alternative hypotheses were proposed, including:

H_{A1}: Commander Island pups display less wide-ranging movements than pups from the Pribilof Islands.

H_{A2}: Commander Island pups display different dive behavior patterns and therefore may use different resources than pups from the Pribilof Islands.

H_{A3}: Commander Island pups prefer different habitats than pups from the Pribilof Islands.

The hypotheses were tested through the following objectives: (1) determine the dive behavior and movement patterns of individuals from a relatively healthy population in the Commander Islands, (2) determine the preferred foraging areas and habitat associations of pups from the Commander Islands population, (3) compare the behavior of pups from the Commander Islands population to other studies of pup behavior in the declining Pribilof Islands population.

Overview of Chapters

A review and update of the global population trends of the northern fur seal population is presented in Chapter II. This chapter described the need for a better understanding of the relationship between the Commander and Pribilof Islands

populations in order to determine whether or not continued declines in the Pribilof Islands would greatly affect other northern fur seal populations, or vice-versa. Simulation models facilitate the evaluation of different mortality rates and scenarios that project future population trends. The inclusion of a dispersal factor among populations is the first attempt to model the effects of emigration from the Pribilof Islands to smaller populations, and to investigate the usefulness of the metapopulation concept in studies of northern fur seals.

Chapters III and IV examine the diving and foraging behavior of northern fur seals from the Commander Islands. In Chapter III, I analyzed data on the depth, duration and time of day that most dives occurred. The frequency of dive behavior also indicated possible peaks in feeding behavior throughout the day.

Chapter IV investigates how stomach-temperature telemetry can indicate more accurately when during the day and where feeding behavior occurs instead of relying on indirect measures, such as diving frequency and individual movement patterns, alone. The salient principle is that the stomach temperature of a warm-blooded animal will drop when it eats food that has a much lower temperature (Andrews 1998). The predominantly cold bodied prey of northern fur seals includes fish and pelagic squid and, therefore, telemetry allowed monitoring of ingestion events as they occurred. These data, combined with those for movement, pup location, and oceanographic features, enabled me to more confidently identify important foraging areas of northern fur seal pups.

Chapter V evaluates movement patterns as indicators of foraging behavior in northern sea otters (*Enhydra lutris kenyoni*) and northern fur seals. Path tortuosity,

compared between adult females and pups, determined how travel to feeding sites was directed. A comparison of the foraging efficiencies between adult females and pups determined how pups refined their search patterns when foraging before they reached adulthood.

Chapter VI describes the habitat associations of northern fur seal pups that migrate from the Commander Islands. I analyzed the relationship between pup locations and several oceanographic features. Associations with oceanographic conditions provide information for comparing the distribution of available resources for northern fur seal pups throughout the north Pacific. Pelagic foragers may prefer areas that are high in chlorophyll-a, which indicates areas of higher productivity and more prey. Top marine predators such as fur seals are linked to chlorophyll-containing phytoplankton in lower trophic levels through trophic links. The main prey of northern fur seals in Bering Island include planktivorous fish such as whitespotted greenlings (*Hexagrammos stelleri*) and Atka mackerel (*Pleurogrammus monopterygius*) (Blokhin, 2006), hence both fish and fur seals are attracted to regions of high phytoplankton concentration and high productivity.

Habitat associations, as indicated by bathymetric features, may also reveal whether individuals are able to direct their movement based on currents or water depth. The satellite tracks of adult northern fur seals are associated with physical and oceanographic conditions such as eddies, chlorophyll a concentrations, sea surface height anomalies (Ream et al. 2005), and distances from the continental shelf (Sterling & Ream 2004). I hypothesized that similar associations occur in pups. Other factors, such

as sea surface height, sea surface temperature, and distances from productive cold-core eddies, also may provide information about habitat preferences of northern fur seal pups.

Chapter VII compares the early migratory behavior of northern fur seal pups from the Commander and Pribilof Islands. The diving behaviors were comparable for the two populations because the parameters chosen for recording the dive depth and dive durations in this study matched the dive recording parameters from previous studies on Pribilof Islands pups. I expected the dive behavior to be similar for both populations, which would show temporal increase in diving skill and the use of similar resources. I used a more qualitative approach, based on the distribution and range of individual pup locations, to compare the habitat use of the Pribilof and Commander Islands pups.

Differences in climatic conditions among the different years for this and previous studies could have affected these comparisons between the two populations, and emphasizes the need for concurrent data collection. However despite such limitations, this study provides important initial insights on the migratory behavior of pups from the Commander Islands population and its potential impact on pup survival.

Conservation Importance

This study looked at the behavior of northern fur seal pups is from a stable population in Russia. Previous studies from the declining Pribilof Island population alone were insufficient to identify factors that may influence pup survival because they lacked a baseline for comparison to a healthy population. Furthermore, international

research is important to behavioral studies of a migratory species because a coordinated management policy among countries may be needed.

Evidence of increased ship traffic or resource extraction in northern fur seal habitat may explain some of the stresses faced by northern fur seals, thus, international agreements are needed in order to attain conservation goals. Northern fur seals, like other marine mammals, may serve as sentinals against problems in lower trophic levels of a marine ecosystem. A better understanding of why a marine predator population is declining could also indicate problems within and among fish stocks, and thus, would be of interest to the international fishing industry. However, the greatest tragedy for the fate of northern fur seals would be to see this species face extinction, not at a time when commercial hunting was rampant and little was known about their biology, but in the present, when this species is protected and decades of research has significantly improved our knowledge about them. The uncertain future of northern fur seals is a reminder that human impacts can be long-lasting and difficult to reverse.

CHAPTER II

POPULATION TRENDS OF NORTHERN FUR SEALS *(Callorhinus ursinus)* FROM A METAPOPULATION PERSPECTIVE

Introduction

Northern fur seals are found throughout the North Pacific with a southern limit at 40˚ N latitude. The two largest breeding populations occur in the Pribilof Islands (PI) and Commander Islands (CI), which currently make up approximately 50% and 20% of the total population respectively (National Marine Mammal Laboratory, unpublished data). The remaining 30% of the population returns to breed in four main areas: Robben Island (RI), the Kuril Islands (KI), Bogoslof Island (BI) and San Miguel Island (SMI). Historically, commercial hunting of northern fur seals for their pelts severely depleted their numbers worldwide. Harvests began on the CI in the late 18th century and soon thereafter on the PI and RI. Increased demand for these pelts motivated the start of pelagic harvesting of seals; a particularly destructive practice in which both males and females were hunted.

The resulting worldwide population decline prompted the creation of the International North Pacific Fur Seal Treaty in 1911, which halted the practice of pelagic harvests, and was one of the more successful management policies allowing northern fur seal populations to recover (Atkinson 1988). The history of commercial hunting of northern fur seals is well documented (Roppel & Davey 1965, Roppel 1984, Schaeffer 1984, Atkinson 1988, Gentry 1998) and shows a pattern that alternates between

indiscriminant hunting and implementation of conservation measures to improve declining stocks. Unfortunately up until 1950, international fur seal policies did not include provisions for research that could improve management decisions, and thus, most decisions were based on poor understanding of northern fur seal population dynamics.

Such was the case between 1950 and 1960 when a management decision was made to allow culling of females as part of a herd reduction program in the PI. Commercial harvests previously targeted juvenile males on shore, but a decline in juvenile males on rookeries was initially attributed to increased intraspecific competition. With the expectation of increasing future harvests of juvenile males, adult females were harvested to reduce the total population size and subsequently reduce competition among juveniles in future year classes. Natural mortality rates were also expected to decrease with reduction in intraspecific competition, but no studies were conducted to support this assumption. The large-scale culling of adult females was followed by a dramatic decline in fur seal populations, particularly in the PI. Since the 1950's the PI population has continued to decline at 6% annually (National Marine Mammal Laboratory unpublished data).

Commercial harvests ended in the 1970's and currently only subsistence harvests are permitted on the CI and PI. Subsistence harvests take less than 2000 animals per year (Angliss and Lodge 2003) and are not thought to contribute significantly to the continued decrease of the PI population. In contrast, other northern fur seal populations

are increasing or relatively stable (National Marine Mammal Laboratory, unpublished data).

Previous studies concentrated on causes of the population decline in the PI, and simulation models suggested that the decline was due to increased mortality caused possibly by entanglement in fishing gear or greater competition for prey resources in common with fishermen (Trites & Larkin 1989). Other suggested sources of mortality included increased predation rates, disease, and habitat loss. However, the previous simulation models omitted any potential for migration among the different breeding locations to affect population size.

The decline in the PI population in the 1950's occurred when previously unoccupied breeding territories in BI and SMI became colonized. Tracking studies on both adults and juveniles from the PI and CI show that individuals range throughout the north Pacific and Bering Sea during a single 2 to 4 month migratory period, and therefore are capable of dispersing to a new location within a year. The overlapping ranges of most of these breeding populations (Fig. 1), and the lack of genetic differentiation among the different breeding locations (Ream 2002, Dickerson et al. 2008), suggest significant flux among the various northern fur seal populations. However, strong site fidelity had been observed in this species, particularly among adult females (Gentry 1998). Therefore, migration presumably occurs mostly among juveniles that may have not yet established an affinity for a particular breeding location.

The use of ecological modeling in this study is an attempt to provide a better understanding of the trends for each of the six main breeding populations of northern fur seals.

Model Objectives

The objectives of this study were to 1) Model historical population trends for the six main populations (PI, CI, KI, SMI, BI and RI) using known life history parameters. 2) Explain current population trends in terms of requisite changes in mortality rates (due to entanglement or predation) or variation in birth rates caused by environmental or intrinsic factors. 3) Model movements among the different populations to examine trends in immigration and emigration, and to identify potential source and sink populations. 4) Model future population trends using different scenarios for predicted changes in mortality rates and in habitat preferences, in order to identify strategies for conservation.

Methods

The model was created using STELLA 9.1.3 (ISEE Systems) with simulations set to occur with a time step (dt) of 1 month. The model started at month 0, which corresponded to December 1929, and ended at month 1008, which corresponded to December 2014. The overall metapopulation model had two main parts: 1) a migration model of flow of individuals among populations, 2) site-specific variants of an age-structured population model that accounted for variation in birth and death rates in each of the six populations.

Migration Model

The immigration and emigration model was used to direct simulated flow of individuals among breeding populations. The flow equations and assumptions of the model were essentially those of Neill et al. (1983) with links among all populations because movement was expected to occur among all populations. However, studies of the migration of northern fur seals for SMI indicated that pups rarely traveled far off the east Pacific coast, which indicated their relatively smaller movements (Lea et al. 2009b). To account for this decreased connectivity for SMI, the habitat quality value for SMI was set relatively low throughout the simulation period.

The direction of flow among populations depended on the habitat quality, which included population preferences. The habitat quality (p_i and p_j) for each paired population set was determined by how long that location was occupied and size of the initial population. The equation for rate of colonization provided by Hanski (1994) was modified to predict the final value for habitat quality (p_i at t = 1008).

$$p_i(0) = \frac{M_i^2}{M_i^2 + y^2}$$

The initial value of p_i for each population was estimated by calculating the ratio of the sizes of the paired populations in 1958, which was the earliest available estimate, and based on percent abundances among islands within the global population of northern fur seals (Gentry 1998). The largest habitat quality value was assigned to the PI, as it was occupied the longest and it initially contained 87% of the world's northern fur seal

population. M_i referred to the initial population size at time 0, and y was calculated by substituting the values for $p_i(0)$ and M_i. The value for y, which was an estimate for the maximum final population size, was then divided by the initial population size (M_i) and converted into a percentage to find the final habitat quality value $p_i(t = 1008)$. The value of p_j was simply the complement of p_i (i.e. $p_j = 1 – p_i$).

In recently colonized locations, the habitat quality value started as 0 before a location was colonized, but slowly increased as animals arrived from other populations. The value p_i was increased by 1% every year until the maximum, or final, value at $p_i(t=1008)$ was reached. However, during El Nino years migration between any two populations was expected to be reduced. Movement from northern populations to southern populations was expected to decrease significantly, following the lack of available prey at lower latitudes during El Nino years (Delong & Antonelis 1991). During such years, the habitat quality value of the southern SMI populations was decreased by 50%, and increased by the same percent in the more northern populations in the CI and PI. After an El Nino year, the habitat quality of SMI returned to its value in the year before El Nino. Once the value of p_i was reached, net flux between the two populations was approximately zero.

The dispersion speed (V) was calculated using the average swim speed of northern fur seals of 48 cm sec^{-1} (Ream et al. 2005), and calculating the expected maximum travel speed for a dt of one month. The maximum travel speed was 1296 km $month^{-1}$ and included no resting period. To account for some resting during migration a

maximum travel speed (V) of 1,000 km month^{-1} was assigned during the two main migratory periods in May and November. A slower migratory speed of 50 km month^{-1} was used at other times of the year. An attempt to use speeds in km h^{-1} was unsuccessful for a simulation run of 100 years because it increased model computing time significantly. The value of each stock population in the migration model was a percentage of the total population, so at any given time, the entire northern fur seal population was set at 100 animals.

Population Model

The population model used an age structured approach that assigned separate parameters by sex after the age of 2 years. Females were expected to live up to 26 years and males up to 11 years (Fig. 2). The PI population was the only metapopulation with a known age structure. The same starting ratio of individuals for each sex and age class was used for all metapopulations, except for the newly colonized BI and SMI metapopulations, for which age structure depended on immigration.

Pups are born annually between May and July, with a peak in births in late June – early July (Trites 1992, Gentry 1998). However, the modeled assumed all pup births occurred in June, which simplified calculations but did not account for the increased mortality of pups born later in the year. Natality for each population depended on the ratio of adult territorial breeding males (aged 9 to 11 years) to breeding females (adults aged 6 to 26). Subadult females (aged 4 to 6 years) also contributed to natality, but with much lower birth rates than adult females. If the ratio of breeding males to females was less than or equal to 4 (i.e., total number of males aged 9 to 11 years / total number of

breeding females aged 6 to 26 years ≤ 4) then an optimal birth rate was used, with the maximum pregnancy rates for each category of adult breeding females assigned values based on the literature (Table 1). If the ratio was less than optimal, a lower pregnancy rate was applied to all categories of breeding females. York (1987) reported slightly higher pregnancy rates in the west Pacific compared to the PI seals, and this was reflected in higher natality rates for populations of the CI, RI and KI.

The pregnancy rates for all populations except Robben Island used an average value for all adults obtained from York and Hartley (1981). RI was the exception because environmental factors, such as ice-formation and current patterns, affected the timing of female arrivals on shore (Ashchepkov et al. 2006). There is a later start to reproduction in those years, which was expected to negatively affect birth rates. Therefore, a temporally variable pregnancy rate was assigned to RI to reflect the decreased birth rates during the years when unfavorable environmental conditions delayed female arrival on shore.

The density dependent effects on pup (0 to 4 months) mortality were included in the model only for the PI, CI and RI. These three populations showed an asynchronous trend of large increases, followed by a sudden decrease in population size. A non-linear density dependent relationship between the number of pups born and pup mortality rates was observed by Fowler (1990). This relationship was used to model pup mortality rates for the PI and RI populations.

The density dependent relationship from Fowler (1990) was:

Pup (0-4 months) mortality coefficient = ae^{bx}. For the PI, a = 1.0173, b = 0.7042, x = number of pups born/150,000 and for RI, a = 0.647, b = 0.07, x = number of pups born/500.

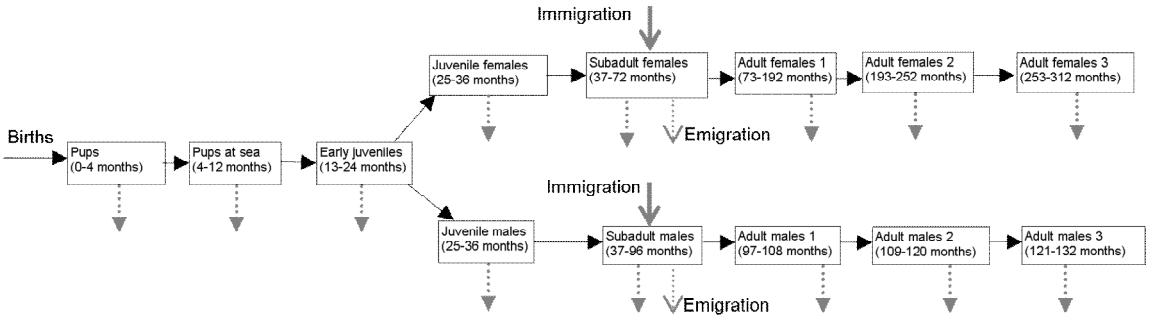

Fig. 2. Age structured population model.

The CI population was assumed to have a density dependent relationship similar to RI; the parameter values used for the CI were: a = 0.8, b = 0.11, x = number of pups born/800. The time frame in which the model was run did not include the period of rapid increase in the CI population (unlike the RI and PI populations), therefore the density dependent relationship was only applied until 1963, after which the CI population appeared to be relatively stable. During the period of stable population trends, the average pup mortality rate of 0.055 was applied.

Table 1. Instantaneous birth and mortality rate coefficients (Z) for each population at monthly intervals. Temporally variable rates are reported as a range of values.

	Pribilof	Commander	Robben	Kuril	Bogoslof	San Miguel
Birth rates if sex ratio <8						
Subadult females	0.17	0.3	0.2	0.3	0.2	0.2
Females 6-16	0.8	0.84	0.85	0.85	0.85	0.8
Females 17-20	0.57	0.57	0.5	0.57	0.57	0.57
Females 21-26	0.098	0.09	0.098	0.098	0.098	0.098
Birth rates if sex ratio >8						
Subadult females	0.09	0.15	0.09 - 0.1	0.1	0.1	0.1
All adult females	0.5	0.6	0.64	0.65	0.54	0.65
Pups 0-4 months mortality	0.02 - 0.25	0.4 – 0.05	0.4 – 0.049	0.055	0.055	0.055
Pups 5-12 months mortality	0.02 - 0.065	0.02 - 0.06	0.02 - 0.06	0.02 - 0.06	0.02	0.02
Early juveniles mortality	0.057 - 0.066	0.057	0.057 - 0.066	0.057	0.057 - 0.066	0.057 - 0.066
Juvenile male mortality						
Natural	0.05	0.03	0.03	0.025	0.035	0.03
Juvenile male entanglement	0.014 - 0.1	0.014 - 0.1	0	0.014 - 0.1	0	0
Juvenile female mortality						
Natural	0.045	0.02	0.02	0.02	0.03	0.03
Juvenile female entanglement	0.014 - 0.1	0.014 - 0.1	0	0.014 - 0.1	0	0
Subadult female mortality						
Natural	0.02	0.02	0.02	0.02	0.02	0.02
Harvest	0 - 0.208	0	0	0	0	0
Entanglement	0.0002 - 0.0003	0.001 - 0.011	0.001 - 0.011	0.001 - 0.011	0.0002 - 0.0004	0.019 - 0.043
Additional mortality	0.0084 - 0.0264	0.01	0.02 - 0.035	0.018 – 0.025	0 - 0.01	0 – 0.04
Subadult male mortality						
Natural	0.017	0.017	0.017	0.017	0.017	0.017
Harvest	0 - 0.022	0 - 0.015	0 - 0.02	0.009 - 0.018	0	0
Entanglement	0.00002 - 0.00003	0 - 0.005	0.0001 - 0.0011	0.0001 - 0.0011	0.00002 - 0.00003	0
Additional mortality	0.0035 – 0.011	0.005	0.002 - 0.0035	0.018 – 0.025	0 - 0.002	0 – 0.02
Female mortality 1						
Natural	0.012	0.01	0.012	0.012	0.012	0.025
Harvest	0 - 0.07	0	0	0	0	0
Entanglement	0.0002 - 0.0003	0.001 - 0.011	0.001 - 0.011	0.001 - 0.011	0.0002 - 0.0003	0
Additional mortality	0.007 - 0.022	0.01	0.02 - 0.035	0.018 – 0.025	0 - 0.02	0 – 0.04

Table 1 continued.

	Pribilof	Commander	Robben	Kuril	Bogoslof	San Miguel
Female mortality 2						
Natural	0.04	0.03	0.04	0.04	0.04	0.04
Harvest	0 - 0.07	0	0	0	0	0
Entanglement	0.0002 - 0.0003	0.001 - 0.011	0	0	0	0
Additional mortality	0.0035 – 0.011	0.005	0	0	0	0
Female mortality 3						
Natural	0.08	0.08	0.08	0.08	0.08	0.08
Harvest	0 - 0.07	0	0	0	0	0
Entanglement	0.0001 - 0.00015	0.001 - 0.011	0	0	0	0
Additional mortality	0.0007 - 0.0022	0.001	0	0	0	0
Male mortality 1						
Natural	0.011	0.011	0.011	0.011	0.011	0.011
Harvest	0 - 0.015	0 - 0.022	0.001 - 0.002	0	0	0
Entanglement	0.00002 - 0.00003	0 - 0.005	0.0001 - 0.0011	0.0001 - 0.0011	0.00002 - 0.00003	0
Additional mortality	0.0035 – 0.011	0.005	0.002 - 0.0035	0.0018 – 0.0025	0 - 0.002	0 – 0.02
Male mortality 2						
Natural	0.02	0.02	0.02	0.02	0.02	0.02
Harvest	0 - 0.015	0 - 0.022	0	0	0	0
Entanglement	0.00002 - 0.00003	0 - 0.005	0.0001 - 0.0011	0.0001 - 0.0011	0.00002 - 0.00003	0
Additional mortality	0.0035 – 0.011	0.005	0.002 - 0.0035	0.0018 – 0.0025	0 - 0.002	0
Male mortality 3						
Natural	0.04	0.04	0.04	0.04	0.04	0.04
Harvest	0 - 0.015	0 - 0.015	0	0	0	0
Entanglement	0.00002 - 0.00003	0 - 0.005	0.0001 - 0.0011	0.0001 - 0.0011	0.00002 - 0.00003	0
Additional mortality	0.0035 – 0.011	0.005	0.002 - 0.0035	0.0018 – 0.0025	0 - 0.002	0
Natural	0.012	0.01	0.012	0.012	0.012	0.025

Immigration and emigration only affected subadult males and females in the model due to strong site-fidelity in this species. Migration rates of up to 25% have been reported for males arriving in non-natal beaches (Lander & Kajimura 1982, Kornev et al. 2008), and adult females are expected to have even lower migration rates and higher site fidelity than males (Baker et al. 1995, Chilvers & Wilkinson 2008). The migration model assumed a more conservative estimate of 10% of subadult females and 10% of subadult males migrating, but to account for higher male migration rates, subadult males in a population were allowed to migrate year round. In contrast, subadult female immigration into a population only occurred during the months of May and June, when they were most likely to join the breeding population on shore. The age-structured population model for any one population only included immigration when there was an increase in the percentage of animals, for that population, from the migration model. Separate immigration inflows were calculated for subadult males and females. Immigration in subadult females was calculated using the equation:

$$\text{female immigration} = \frac{[(D(t) - D(t\text{-}1))*(\text{worldwide subadult female population})]}{1000}$$

where D(t) is the stock size of the population of interest from the migration model at time t, and D(t-1) was the stock size of the same population one month earlier. The change in population density was divided by 100 to convert it to a percent change, and then multiplied by one tenth to simulate only 10 percent of the worldwide subadult female population that did not have strong site fidelity. The same calculation was

applied to calculate male immigration using the worldwide male subadult population, and the percentage of population increase in subadult males.

If there was movement out of the population, the decrease in the percentage of the population from the migration model was applied as an outflow of the subadult male and female stock by converting it from an integrated percentage decrease, to an instantaneous mortality rate. Unlike immigration, emigration was allowed to occur at any time during the year.

The harvest rates combined pelagic and shore harvest numbers that were converted into a harvest mortality coefficient using estimates of population size from the literature. The greater percentage of subadults in the harvests (York & Hartley 1981) was reflected in the model by doubling the average sex-specific harvest rates for the subadult age stock. However, I used the average sex-specific harvest rates for the adult breeding stocks. Harvest rate information for animals from the CI and RI were obtained from Lander and Kajimura (1982). No harvest rate information was available for the KI, so 90% of the harvest rates from nearby RI were used instead. No female harvests occurred in the western Pacific populations, and therefore the female harvest mortality rates were excluded in the model for those metapopulations.

Mortality from entanglement for juveniles and adults was estimated using published values (Fowler & Ragen 1990, Angliss & Lodge 2003). Juvenile entanglement rates were higher than those for adults (Sinclair & Robson 1999), and higher entanglement rates were also observed in the west Pacific compared to the east Pacific (Kuzin et al. 2000).

Increases in historical average intrinsic mortality rates were accounted for by including temporally variable mortality rate coefficients for all subadult and adult males and females. These rates accounted for mortality caused by predation, disease and starvation which were thought to increase northern fur seal mortality significantly in the last 50 years.

Model Validation

The model was validated using pup counts for each population. Pup counts have been the only reliable estimate of population size because all pups born in a cohort can be counted on shore, whereas a portion of all other age classes may remain at sea during the breeding season. The PI pup counts were the combined pup counts from St. George and St. Paul island from 1948 – 2005 (National Marine Mammal Laboratory 2005). BI pup counts were obtained for the years 1980 – 1989 (Loughlin & Miller 1989), and from 1992 – 2002 (Angliss & Lodge 2003). SMI pup counts were available from 1969 – 2003 (Delong 1982, Melin et al. 2005), and the CI, KI and RI pup counts for 1958 – 2006 were obtained from the National Marine Mammal Laboratory (unpublished data).

Correlations between actual pup counts and simulated numbers of pups born were tested by calculating the Pearson's correlation coefficient for the months when pup count data were available, and the significance of the correlations were calculated.

The size of each population was calculated using two methods. Method 1 is used by the National Marine Mammal Laboratory to estimate the total population size by multiplying pup counts by an expansion factor of 4.475. This factor which was calculated using an age structured population model (Lander 1981), but it has not been

recently validated. Method 2 used the population simulation model to calculate the total population size by adding the total number of individuals from each sex and age group, and did not require a correction factor.

Future Population Scenarios

The trends for all populations except the PI appear to be stable or increasing (National Marine Mammal Laboratory, unpublished data). Therefore, simulations of future population size focused only on the PI. Birth rates were increased up to 10%, and the adult and pup mortalities were each decreased by up to 20%. In all scenarios, the mortality rates were not reduced below the reported natural mortality rates. The time taken for the PI population to reach 1.5 million animals was investigated for a maximum simulation period of 2,000 months, allowing estimates of recovery time only up to 83 years from the present (i.e., year 2093).

Results

Pup Counts Validation

The simulation model provided the closest fit for number of pups born in the first 700 months (years 1930 to 1988) for growing populations in SMI, BI, and the KI (Fig. 3). The correlations between actual and simulated pup counts for all six populations were significant (Table 2). The lack of available data on pup counts on the CI before month 300, represented as zero actual pup births (dashed line) (Fig. 3), resulted in a poor model fit.

The model predicted twice as many animals on BI as current population estimates, which are based on pup counts conducted in 1995 (Angliss & Lodge 2003). Simulated pup births were more similar to actual counts on SMI.

The model simulated a more dramatic decrease in births on the PI (Fig. 3a) than actual data indicated during the period of female harvests (month 400), but the model also predicted a quick recovery after female harvests ended.

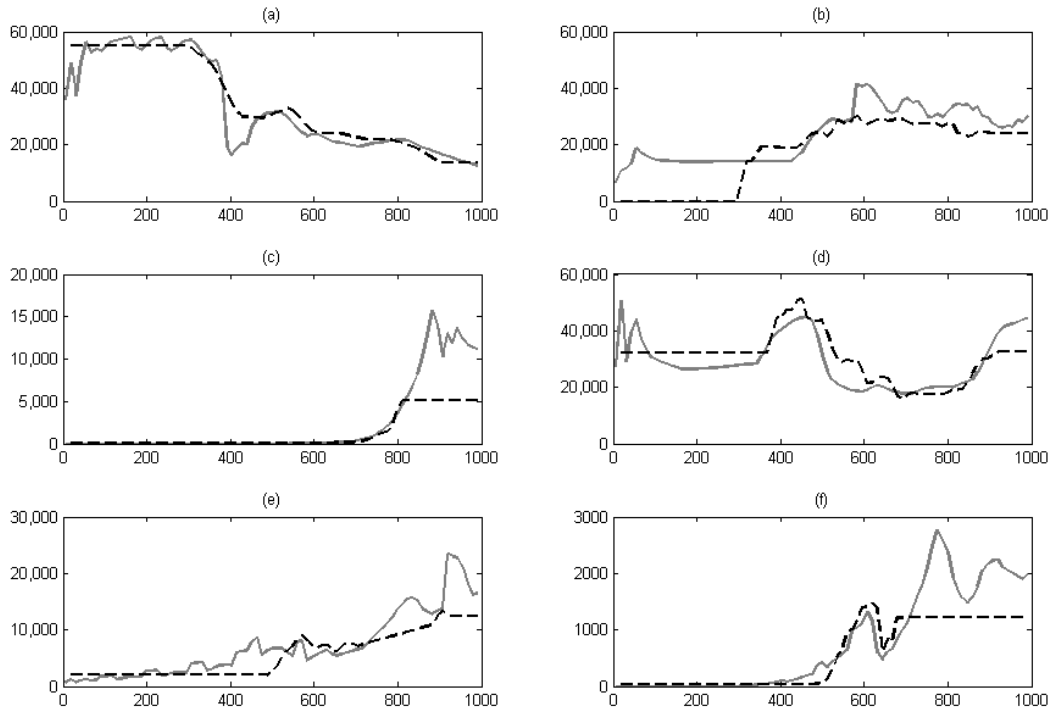

Fig. 3. Number of pups born from the model (solid line) and pup counts (dashed line) for a) Pribilof Islands, b) Commander Islands, c) Bogoslof Island, d) Robben Island, e) Kuril Islands, and f) San Miguel Island populations.

Table 2. Pearson's correlations between actual and simulated pup counts for all populations. Test for significance (p) is two-tailed.

Population	N	Pearsons r	p
Pribilof	60	0.927	<0.0001
Commander	58	0.841	<0.0001
Robben	53	0.817	<0.0001
Kuril	43	0.817	<0.0001
Bogoslof	38	0.919	<0.0001
San Miguel	53	0.817	<0.0001

Total Population Estimates

Both methods overestimated population sizes, although method 1 generally estimated population sizes that were closer to reported values (Table 3). Although population sizes were overestimated, the percentage distribution of animals among the six populations was close to values reported in 2004. Method 1 and 2 were also better at predicting population sizes for the smaller populations in SMI, BI, KI and RI compared to CI and PI.

Method 1 overestimated the population sizes by 16% and 17%, in 1992 and 2004 respectively, and was significantly different from the reported population sizes (Wilcoxin signed rank test, $Z = -2.589$, $p = 0.01$). Method 2 overestimated population sizes by 18% and 39%, in 1992 and 2004 respectively, and was also significantly different from the reported population sizes (Wilcoxin signed rank test, $Z = -3.059$, $p = 0.002$). However, estimates from both methods were not significantly different from one

another (paired samples t-test, t = -1.51, DF = 11, p = 0.159, mean differences = 21752.2, SE mean differences = 14402.7).

The reported estimates for the global northern fur seal population size decreased 12% from 1992 to 2004, and this was also detected by method 1. However, an increase of 4% in the global population size was observed using method 2, which also predicted the largest current global population.

Migration Model

The population increase in BI from 1980 – 1988 (months 600 to 700) showed a significant contribution from immigrant animals ranging from 50 to 200 immigrant females yr^{-1} (Fig. 4). On SMI, modeled immigration contributed to population growth from 1955 – 1963 (months 300 – 400), with net female immigration of 20 to 150 females yr^{-1} (Fig. 4). There was no increase in female immigrants into RI during the period of large population growth (month 700 onwards). The largest rates of emigration from the PI occurred from 1930 – 1980, and subsequently decreased, as the PI population decreased.

Table 3. Percentages of global northern fur seal population from the model and reported values for 1930, 1992 and 2004. Numbers in parentheses refer to total number of animals.

	Reported 1930 population	Model 1992 population Method 1	Model 1992 population Method 2	Reported 1992 population	Model 2004 population Method 1	Model 2004 population Method 2	Reported 2004 population
Pribilof Islands	87	64 (929,843)	66.8 (980,224)	74.4 (928,997)	53.4 (684,793)	55.4 (846,891)	52.5 (577,500)
Commander Islands	7	23.1 (335,835)	20 (294,592)	17.2 (214,768)	23.1 (296,093)	20.1 (307,445)	20.6 (226,600)
Kuril Islands	0	5.8 (84,385)	6.8 (100,015)	3.8 (47,449)	8.4 (107,136)	9.5 (144,749)	10.2 (112,200)
Bogoslof Island	0	0.37 (5,410)	0.37 (5,483)	0.2 (2,497)	4.4 (56,058)	5.2 (79,354)	4.5 (49,500)
Robben Island	6	6.1 (88,831)	5.4 (79,397)	3.8 (47,449)	10.1 (129,712)	9.2 (140,712)	11.5 (126,500)
San Miguel Island	0	0.65 (9,453)	0.55 (8,134)	0.6 (7,492)	0.67 (8,636)	0.67 (10,215)	0.7 (7,700)
Total		1,453,757	1,467,844	1,248,652	1,282,428	1,529,366	1,100,000

Reported percentage values for 1930 were obtained from Garshelis (1998), and data for 1992 and 2005 were obtained from National Marine Mammal Laboratory (2005). Stock size for the Pribilof Islands in 1992 and 2004 were obtained from Antonelis et al. (1994) and Anglis and Lodge (2004), respectively.

Future Population Scenarios

The different scenarios of changing rates of mortality and births successfully stopped the declining population trend (Table 4). Despite stabilizing the population, not all scenarios allowed the PI population to recover. The fastest recovery occurred by decreasing adult female mortality rates by 20% (from 33.5% to 26.8% annual mortality; Table 4), which took the PI population approximately 43.1 years from the present to reach 1.5 million. Reduction of pup mortality rates by 20% (from 41 % to 32 % annual mortality), and adult female mortality rates by 10% would take the population more than 80 years to recover. Increasing birth rates alone by 20% did not stop the declining population trend, but increased birth rates together with reductions in pup and adult mortality rates allowed the population to recover. A 10% reduction in each mortality rate for adult females, males and pups resulted in a slow recovery period (> 83 years).

Allowing the model to run for 2,000 months at the current rates of mortality allowed the PI population to decrease to 51,000 animals (method 2), and reduced the number of animals migrating to other populations, but no noticeable effects on the trends of any other population were predicted.

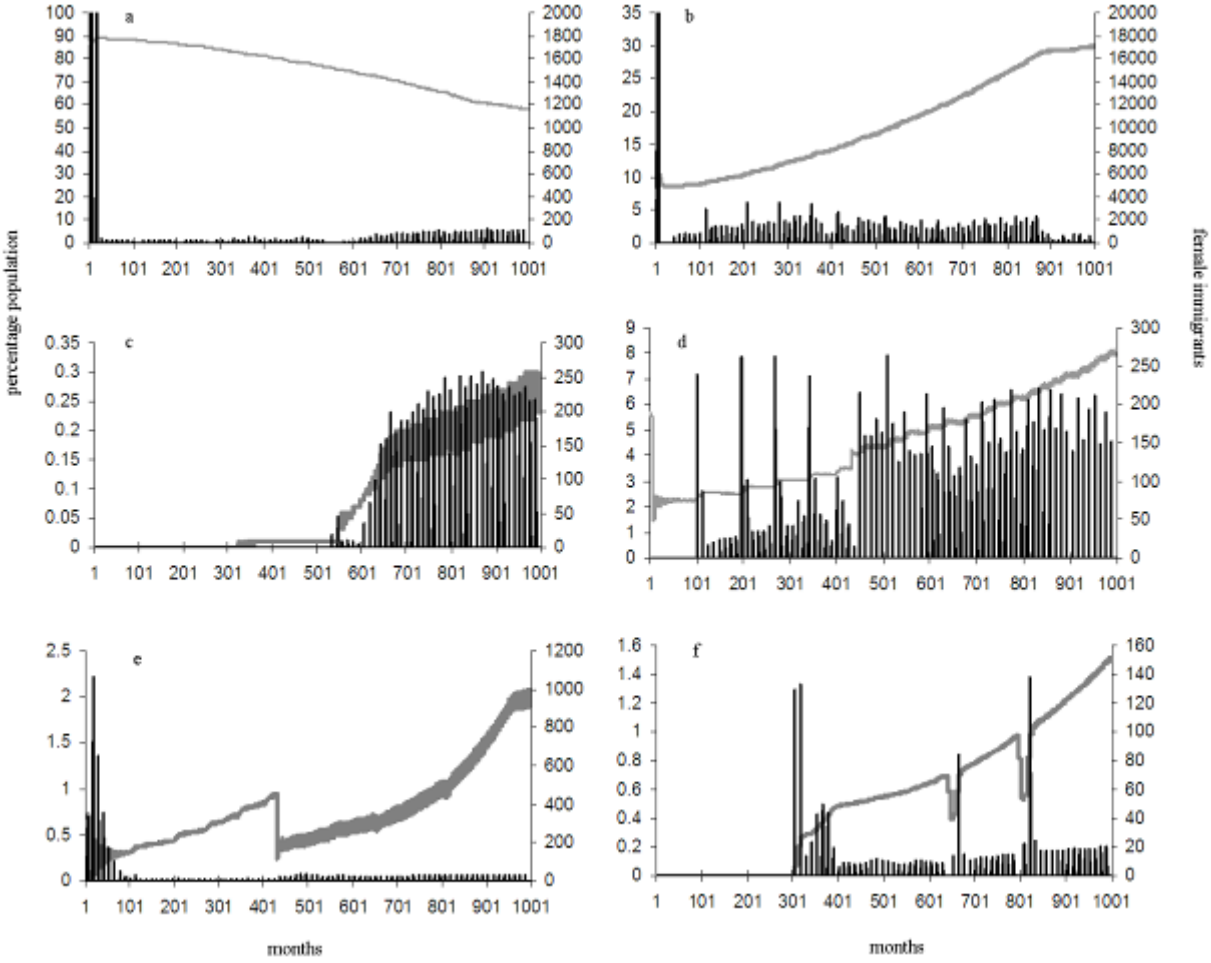

Fig. 4. Number of female immigrants (black lines) and migration model's percentage of the worldwide population (grey lines) for a) Pribilof Islands, b) Commander Islands, c) Bogoslof Island, d) Robben Island, e) Kuril Islands, and f) San Miguel Island.

Table 4. Percentage changes in mortality and birth rates needed for population recovery.

Pup mortality	Juvenile mortality	Adult female mortality	Adult male mortality	Birth rates	Time to reach 1,500,000
-	-	-20	-	-	517 months
-	-	-10	-	-	NA
-20	-	-10	-	-	> 1000 months
-20	-10	-10	-10	20	177 months
-20	-	-10	-10	20	>1000 months
-10	-	-10	-10	-	NA
-20	-10	-10	-10	-	349 months
-10	-10	-10	-10	-	>1000 months

Discussion

An understanding of a species' population dynamics is needed to accurately estimate population size for management purposes. The accuracy of predicting the reported population size was not very good using methods 1 and 2 that both overestimated the reported population sizes. However, the reported population sizes are calculated using method 1 (expansion factor times pup number), and a true count of all individuals can only be obtained through a simulated population model (method 2) where all individuals can be accounted for. The current method of estimating population size (method 1) generally underestimated the size of the simulated population (calculated using method 2). However, because there was no significant difference between methods 1 and 2, the current method used can be considered a reliable estimator of population size, although the results may not be accurate.

Model Fit

The accuracy in simulating the magnitude of population size was more difficult than simulating the overall population trends, and the model tended to overestimate the sizes of subpopulations. The strong correlation in pup births and population trends indicated that the model captured the main processes affecting population size, although the magnitude of these processes may not be accurate.

Particularly high population estimates were obtained for the western Pacific stock (CI, KI, and RI) which probably resulted from the absence of data on birth rates in those populations. Instead, the model had to rely on birth rate estimates for the PI, which may have inflated the simulated number of annual births. Birth rates are also known to change annually (Abegglen & Roppel 1959), and the model only varied birth rates according to the sex ratio between adult females and males. A closer fit to pup counts could be obtained using a more stochastic range of birth and death rates, particularly for the western Pacific stock, where there are currently data deficiencies.

Poor model fit was also observed during periods of high population growth, as seen in the pup count trends for the KI population. This result was not caused by poor model input from the migration model, but rather by population momentum from model parameters since the same pattern was observed even after removing any immigration or emigration. The population dynamics of northern fur seal populations well below estimated carrying capacity were not well captured, and it is unknown why smaller northern fur seal populations in the western Pacific take so long to grow.

The influence of density dependent factors on population growth could play a role in the early growth trends of small populations. However, the density dependent effects on population size focus on how large populations face decreased population growth caused by increased mortality (Rotella et al. 2009), but no northern fur seal studies suggest a low-density effect on mortality rates. In a scenario of low-density effects, there may be a threshold population size below which a population may suffer from increased mortality rates (e.g., inability to overcome predation or disease mortality rates). A benefit of larger population sizes includes the dilution effect of large aggregations that can decrease predator caused mortalities (Wrona and Dixon 1991). In northern fur seals, large aggregations are usually found only on land during the breeding season, and land predators (apart from humans) are uncommon. A dilution effect on land may be beneficial to pups consumed by Arctic foxes, but no evidence currently suggests high predation rates from this species.

A more likely scenario for increased pup mortality in small populations is increased marine predation. Pups are known to leave the rookery in large groups following storm events (Lea et al. 2009a) and such swimming aggregations may attract marine predators. Groups of dispersing northern fur seal pups from smaller populations may suffer higher mortality rates from marine predators than pup aggregations dispersing from larger populations.

Low densities of northern fur seal populations in SMI also suffer higher mortality rates from hookworm disease, and pup mortality from this factor is thought to depress population growth (Melin et al. 2008). The incidence of hookworm disease in

the western Pacific populations is unknown, but this could have been a factor in slowing population growth in the KI and RI populations (National Marine Mammal Laboratory, unpublished data).

Alternatively, the effects of density-dependent dampening of population momentum could explain the low observed pup counts during periods of population growth. In vertebrates with long generation times, a reduced fertility rate in a growing population with an excess of immature animals compared to adults can actually slow the growth of a population. The effects of population momentum caused by reduced fertility rates in growing populations can even cause the population size to decrease before it stabilizes (Koons et al. 2006). Reduced adult fertility rates modeled for the Robben Island population increased model fit, but may not have been large enough to explain the depressed population growth period from 1980 to 2000.

In contrast, the stable or decreasing population trends were well represented by the model. The effect of female harvests on the PI was particularly evident in both the model results and the observed decline in pup production rates (month 400), which subsequently resulted in the declining trend for pup count. The stochastic annual effects on either mortality or fertility rates made the trends in CI pup production more difficult to simulate, although the simulated and actual pup counts both oscillated around 60,000 animals. The stable population trend for SMI was obtained by setting carrying capacity at current population estimates, but for BI, the slightly declining trend in the simulated model was likely attributable to outdated information for pup counts. BI pup production was last observed increasing 12% annually (Banks et al. 2006), but since 2005 the

population has been reported as stable, even though no new pup counts have verified that the BI population is no longer increasing. More recent pup counts on BI would help validate this assumption.

Future Pribilof Islands Population Trends

Increased adult and juvenile mortality were cited as the cause for the current PI decline in the past (Trites & Larkin 1989, Trites 1989), although there has been some argument about which factors contribute most to mortality (Trites 1992b, Fowler et al. 1994). The model simulated three types of mortality for distinct groups of adults and juveniles: 1) estimated natural mortality, 2) entanglement mortality, 3) an additional mortality rate (which included the effects of disease, fisheries interactions and predation).

The current annual mortality rates caused by additional factors, such as predation and prey limitation, allowed continued momentum for population decline even when these rates were kept constant, and entanglement-caused mortality decreased from 1995 onwards. Reversal of the declining population trend required a decrease in adult and pup mortality rates of at least 10%, and up to 20% in order to produce population recovery. The effects of increased fertility alone did not stop the declining population trend, nor did it allow the population to reach its pre-harvest size unless mortality rates also were decreased.

The main factors contributing to high PI mortality rates remain speculative, but food limitation is thought to be a major factor. Observed changes in the preferred prey of northern fur seals from the Pribilof Islands were similar to changes observed in other top

predators, implying that a change in the prey base (Sinclair et al. 2008) could be affecting the ability of northern fur seals to capture food. Trites (1992b) reported evidence from the mid-1980's that pointed towards increased prey availability during the months of female attendance (June – October), but also pointed out that little was known about prey availability once animals left their rookeries in November. During their first few months at sea, pups may be particularly susceptible to increased mortality from starvation.

In the last few decades, an increased dependence on pollock (*Theragra chelcogramma*) has been observed in the diets of northern fur seals and other predators, such as black legged kittiwakes (*Rissa tridactyla*), red-legged kittiwakes (*Rissa brevirostris*), thick-billed murres (*Uria lomvia*) and common murres (*Uria aalge*), from the PI (Sinclair et al. 2008). Some rookeries in the CI have also shown an increased dependence on pollock (Blokhin 2006) in the last five years. This increased inter- and intraspecific use of walleye pollock also coincides with increased commercial fishing for pollock and leads to a hypothesis of food limitation.

Another factor being investigated as a possible major cause of northern fur seal mortality is increased predation by killer whales (*Orcinus orca*). Studies on Steller sea lions (*Eumetopias jubatus*) in British Columbia and Alaska suggest that sea lion adults and juveniles were most susceptible to killer whale predation (Heise et al. 2003), and observations of predation by killer whales in the CI reported that only juveniles and adult male sea lions were being hunted (Mamaev & Burkanov 2006). In contrast, the current northern fur seal population declines observed in the PI requires increased

mortality of adult female and pups, but based on current reports of orca predation events, females and pups are not considered prey targeted by killer whales.

Migration Model

Payne (1977) showed that large populations of Antarctic fur seals (*Arctocephalus gazella*) can increase colonization of new areas, and Bradshaw et al. (2000), showed similar results for New Zealand fur seals (*Arctocephalus forsteri*). The model in this study did not predict when colonization should begin, but instead, used known dates when fur seals were first observed in an area to simulate the beginning of migration to or from a population. A limitation for this method is that the potential impacts of colonizing new areas in the future could not be investigated. Despite this caveat, the migration model provided useful information on the population growth in newly colonized areas.

The effects on population size caused by migrant animals were only observed in the early population growth phase on SMI and BI. Both of these populations relied heavily on immigration to initiate and increase population growth, but only for the first eight years, after which population momentum allowed population growth to occur without increasing the number of immigrants. Despite the fact that adults aged 6 years and older were reported as immigrants in BI (Loughlin & Miller 1989), the model's use of only subadult migrants sufficiently captured the high growth rates observed in BI. Instead of the reported growth rates of 57% yr^{-1} (Loughlin & Miller 1989), the model predicted population growth rates of 50% yr^{-1}. These high population growth rates greatly exceed the expected population growth rates of 8.12% $year^{-1}$ (Gerrodette et al.

1985), and highlight the importance of immigration in small populations of northern fur seals.

Large, stable populations of northern fur seals did not show much impact from immigration or emigration, which supports the current idea of referring to the main breeding populations as separate populations rather than a metapopulation. Increases in subadult male and female immigration in the PI modeled during the current population decline was not high enough to stabilize population trends, and also confirmed that emigration does not strongly contribute to the current trend.

In RI, the lack of large numbers of immigrant animals during the period of high population growth indicated that immigration did not play a large role in explaining the population growth in the late 1980's. Periods of high immigration in the KI also did not appear to affect population growth during the early to mid-1930's, and a similar, small effect on population growth was observed in the CI during early periods of simulated population growth.

Conclusions and Conservation Implications

The metapopulation approach to modeling northern fur seal populations was used to understand how the declining PI population would affect other northern fur seal populations. The migration model predicted that movement among populations significantly affected only small, growing populations during the first 8 years of colonization. After this period, northern fur seal populations can be stable without immigrants. On the other hand, immigration alone is unlikely to stop the declining population trend on the PI, whereas a 10 % reduction in mortality rates can stop and

stabilize the declining population trends. However, population recovery will require up to 20% reductions in both adult and pup mortality rates.

Comparative studies on adult and pup survival rates from different populations, and more information on the changes in prey availability are needed to improve management plans for northern fur seals. A better understanding of northern fur seal mortality factors, and subsequently how to reduce them is needed to allow populations to recover. In particular, more research is needed on pup and adult female survival at sea, because current mortality rates calculated for animals on shore are negligible.

CHAPTER III

EARLY DIVING BEHAVIOR OF NORTHERN FUR SEAL (*Callorhinus ursinus*) PUPS FROM BERING ISLAND, RUSSIA

Introduction

Northern fur seals (*Callorhinus ursinus*) are one of the few pinniped species whose commercial importance provided some early records of pelagic behavior. Information on the range of these animals was first gathered in 1896 with the help of pelagic sealers (Kajiimura 1980), but scientific interest in the pelagic lives of northern fur seals did not resume until 1948 (Kenyon & Wilke 1953) when the first research cruises were dedicated to identifying the densities and occurrence of northern fur seals at sea.

Despite early records of the surface behavior of northern fur seals, little was known about the diving behavior of animals at sea. A breakthrough in the study of marine mammal diving behavior occurred with the advent of TDR (Time Depth Recorder) technology. The early TDRs recorded depth profiles and frequency of dives (Kooyman 1965) for short periods of time, but the size of the devices restricted their use to large animals such as adult Weddell seals. In the 40 years since those early mechanical instruments, the technology has been transformed by the advent of miniaturized electronics, the subsequent availability of microprocessors, and solid state memory that now enable months of digital recording and very small instruments that can be used on animals weighing less than 3 kg (Kooyman 2004).

Until recently, most research on diving behavior by fur seals focused on parturient adult females (Goebel et al. 1991, Gentry 1998). Several diving strategies have been identified in adult females including: shallow, mixed and deep diving (Goebel et al. 1991). These strategies depended on whether foraging occurred in coastal, pelagic on-shelf, or pelagic off-shelf domains. However, not all sex and age classes within a species behave similarly (Boyd et al. 1998). For example, among northern fur seals from the Pribilof Islands, juvenile males generally made more dives during the day time (Sterling & Ream 2004) compared to adult females that dove mostly during night time and evening. These differences may point to differences in foraging strategies or the use of different prey resources.

The diving behavior of northern fur seal pups has been investigated only recently. Unlike parturient females that behave as central place foragers that return to shore between foraging trips, pups may remain at sea for up to two years during their first winter migration before returning to shore. Tag losses made it difficult to study pups at sea until satellite technology allowed data to be transmitted without recapturing the animal. Depending on the type of data recorded, most archival tags do not have enough battery life to transmit location data for more than one year, and externally attached tags also are likely to fall off after the annual molt. These issues limit the length of time that pups can be tracked at sea. However, dive data have been successfully transmitted via satellite for periods of up to 8 months in some studies (Lea et al. 2006).

The highest mortality rates experienced during the lifetime of northern fur seals are experienced during this early pelagic period of a pup's life, but relatively little is

known about their behavior during this life stage (Gentry 1998). A study on the early diving behavior of pups migrating from the Pribilof Islands described progressively more frequent and deeper dives by pups during the migratory period (Baker 2007). Prior to leaving the rookery, dives by pups occurred mostly during the day, and were relatively shallow. Such behavioral changes suggested a learning period during which pups improve their diving skills. The lack of deep diving by pups prior to leaving the rookery also suggested that pups have little to no experience foraging (Baker & Donohue 2000), and thus, must quickly acquire foraging skills when they begin their winter migration.

The focus of this study was on the diving behavior of pups migrating from Bering Island (BI) to determine if they had a similar learning stage to that of pups from the Pribilof Islands (PI). Differences in the diving behavior of pups may provide information on diving strategies and resource use. The objectives of the study were to: (1) determine the length of time needed for Commander Island pups to reach their maximum recorded dive depth, (2) determine whether time of day influenced maximum dive depth, dive duration, or diving frequency (3) determine whether travel speed or frequent changes in travel direction were correlated with diving behavior, and (4) identify whether individual pups showed variations in their diving strategies, similar to that observed in adult females.

Methods

Study Site and Animals

Thirty five (17 male and 18 female) northern fur seal pups were captured at Severno-Zapadnoe (northwest) rookery on Bering Island, Commander Islands, Russia (*ca*. 55.29°N, 165.77°E) between 30 and 31 October, 2007. Animals were captured just prior to departing the rookery in late October or early November. Animals were weighed using an electronic scale and measured (i.e., standard length and girth). Pups were then physically restrained and anesthetized with isoflurane for up to one hour. Each pup had an Mk10-AL satellite-linked time depth recorder (SLTRDR, Wildlife Computers, Redmond, WA) glued to the fur on its back using epoxy. The animals were allowed to recover before they were released back onto the rookery, and all tagged individuals began their winter migration within the following three weeks.

Satellite-linked Dive Data

Service Argos satellite system was used to track the movements of satellite-tagged fur seals, and receive data on diving behavior. The telemeters transmit ultra-high frequency (UHF) radio signals to Argos receivers on five National Oceanic and Atmospheric Administration (NOAA) TIROS-N weather satellites. The satellites are in sun-synchronous polar orbits. To conserve power, transmissions were limited to times when the fur seals were at the surface. The tags were programmed so that no transmissions occurred between 1001 – 1359 UTC each day when satellite coverage was low (i.e., pass duration less than *ca*. 2 min, Fig. 5). Locations were determined by

Service Argos from doppler shift of tag transmissions created as the satellite passed overhead.

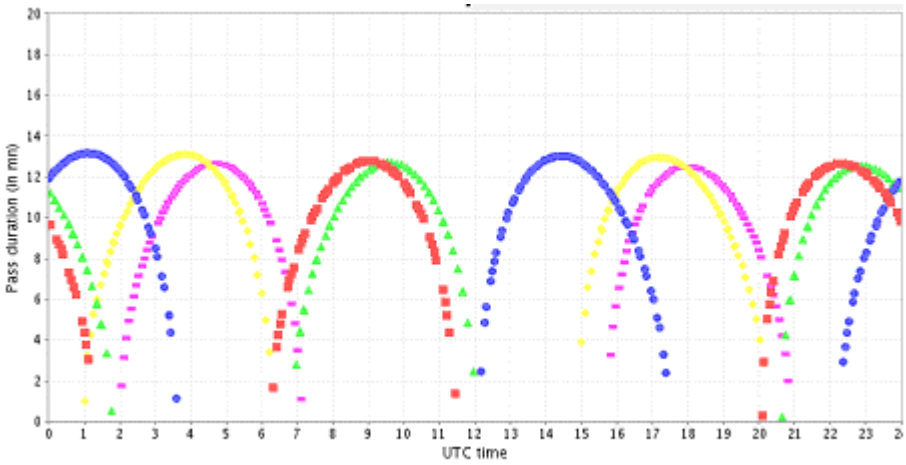

Fig. 5. Satellite coverage over Bering Island at different times of day.

The depth range for the satellite telemeter was 4 to 500 m, with a resolution of 2 m. For each dive, the maximum depth and the duration were binned into histograms and partitioned into 6-h periods corresponding to local time for night (2200-0359), morning (0400-0959), day (1000-1559) and evening (1600-2159). The satellite telemeter was set to record these different time periods corresponding to local hours (-12 UTC), but data records were programmed in UTC. Times of day for the data were later readjusted to local time for the analysis and interpretation. All references to time of day in the analysis are local time. The ranges for the ten depth histogram bins were (upper depth limits): 2 m, 5 m, 10 m, 20 m, 35 m, 50 m, 75 m, 100 m, 125 m, >125 m, and ranges for the duration histogram bins were (upper duration limits): 15 sec, 30 sec, 60 sec, 90 sec, 120

sec, 150 sec, 180 sec, 210 sec, 240 sec, >240 sec. A maximum of 255 dives could be recorded in each histogram bin during a 6-h period each day. However, it was likely that whenever 255 dives were recorded, more than 255 dives had actually occurred in that particular histogram bin. Data were stored in a transmit buffer until it could be transmitted to satellites while the animal was at the surface.

Data Analysis

Dive data from Service Argos were decoded using WC-AMP Version 1.2.15 software from Wildlife Computers. Data for dive depth that were recorded for at least three months were used to determine the rate of maturation of diving ability. The proportion of dives in each dive depth and dive duration bin were calculated for individual pups and used to find differences in the means across all pups for: number of dives, dive depth and dive duration over time (weeks 1 to 18). Two sample Kolmogorov-Smirnov tests using SPSS 15.0 software were used to test for differences in the proportion of dives between consecutive weeks for each dive depth and dive duration bin.

Estimates of average dive depth were calculated using the mid-point of the depth range for each histogram bin. In bins that were subject to overfilling (e.g. 1 to 2 m, 2 to 5 m), this method greatly underestimated their contribution to the dive depths. This issue potentially skewed average dive depths towards deeper dives, since those histogram bins were never filled. Comparisons of average dive depth between males and females were calculated using a Mann-Whitney U test for non-normally distributed samples of dive data.

The diving focus (F) was also calculated for each 6-hour period during each month, from November to February (Frost et al. 2001), for all animals combined. The purpose of a diving focus is to determine if any one particular depth bin was dominant during each 6-hour time period for each month. F was calculated using the equation:

$$F = \sum \{ n_i (n_i - 1) / [N(N-1)]\}$$

where n is the number of dives in each depth bin, and N is the total number of dives (Frost et al. 2001) for all animals combined. A dominant depth bin is usually determined for values of $F > 0.5$. However, when more than two depth bins are compared, values of $F > 0.5$ may only occur if the dominant depth bin contains at least 3 times the number of dives as the second most frequent depth bin.

Satellite track locations were filtered using the David Douglas filter for SAS to determine the best daily pup locations. The filter used a rate coefficient to calculate turn angles from three consecutive points (A –B–C). At any stage in the track, the rate coefficient filter evaluated the distance from A to B, and B to C, and calculated the acute angle ABC. Using a rate coefficient of 25, which was recommended for marine mammals (Douglas Argos Filter Program Manual 2006), all turn angles less than 60 degrees resulted in the removal of point B along the track. The filter was also used to remove consecutive locations > 3 km apart and sustained travel speeds of > 7.2 km h^{-1}. All Argos location points of class 2 or better (accuracy within 500 m radius) were retained. Travel speeds and frequency of changes in turn angles from the best daily locations of each pup were used to determine whether changes in diving behavior were

related to decreased directional swimming (i.e., less swimming in one direction at relatively high speeds).

The numbers of dives per day by duration and depth categories were determined for each individual to identify differences in foraging strategies among individual pups. These data were plotted as the proportion of dives at each depth for each time period (dawn, day, dusk, night) between the months of November 2007 and March 2008.

Individual differences in diving behavior were difficult to classify as unique strategies because so few dive parameters were available. K-clusters analyses are typically used when TDR data are available (Schreer et al. 1998), and often more than 10 dive variables such as dive profile shape, bottom time, or speed, are used to classify diving strategies. In this study, only time of day and dive depth were used to classify dive strategies as shallow, deep or mixed dives. Since dive durations were collected independently from dive depth, we could not associate dive duration with dive depth. Categorical differences in dive depths over time were identified in a 2-step cluster analysis using SPSS 15.0, which determined if individual diving strategies could be identified from preferred dive depth and time of day when most diving occurred. Clusters were identified using the proportion of dives an individual spent in each depth category during each time period (morning, day, evening, night). Pups that transmitted dive depth data for less than 3 months were excluded from this analysis.

Results

Dive Durations

Over 50% of dives lasted < 15 sec, and at least 70 % of dives lasted < 1 min during the migratory period tracked (October 30, 2007 to March 4, 2008). Mean dive duration showed significant increases in the proportion of dives for all dive duration bins during the first two weeks ($p < 0.05$ for all duration bins), but no significant changes in the proportion of dives in any duration bin were recorded after week 7 (Table 5). However, a steady increase in number of dives lasting $\geq$ 90 sec began at 4 weeks, after which there were some fluctuations in the average daily dive durations (Fig. 6). The average dive duration also showed a cyclical trend of shorter dives during the full moon phase, and longer dives during the new moon phase (Fig. 6).

Differences in the average daily proportions among dive durations varied over time, and may have been related to differences among individuals. As individuals spent more time at sea, fewer pups transmitted dive duration data, and over half the pups stopped transmitting duration data after January 16, 2008 (Table 5). The impact of skewed average dive duration and depth data towards fewer individuals, after mid-January, is presented in the section on individual dive behavior.

The effect of time of day on mean dive duration across pups showed a relatively consistent pattern throughout the tracked migratory period. The lowest proportion of dives occurred during the day, and greater proportions of dives occurred during the evening, night and morning. In particular, dives lasting $\geq$ 90 sec were almost never recorded in the daytime (Fig 7). From week 8 onwards (9 December 2007), there was an

increase in mean number of dives lasting 16 to 60 sec during morning hours, but the longest dives (≥ 90 sec) still occurred during evening and night.

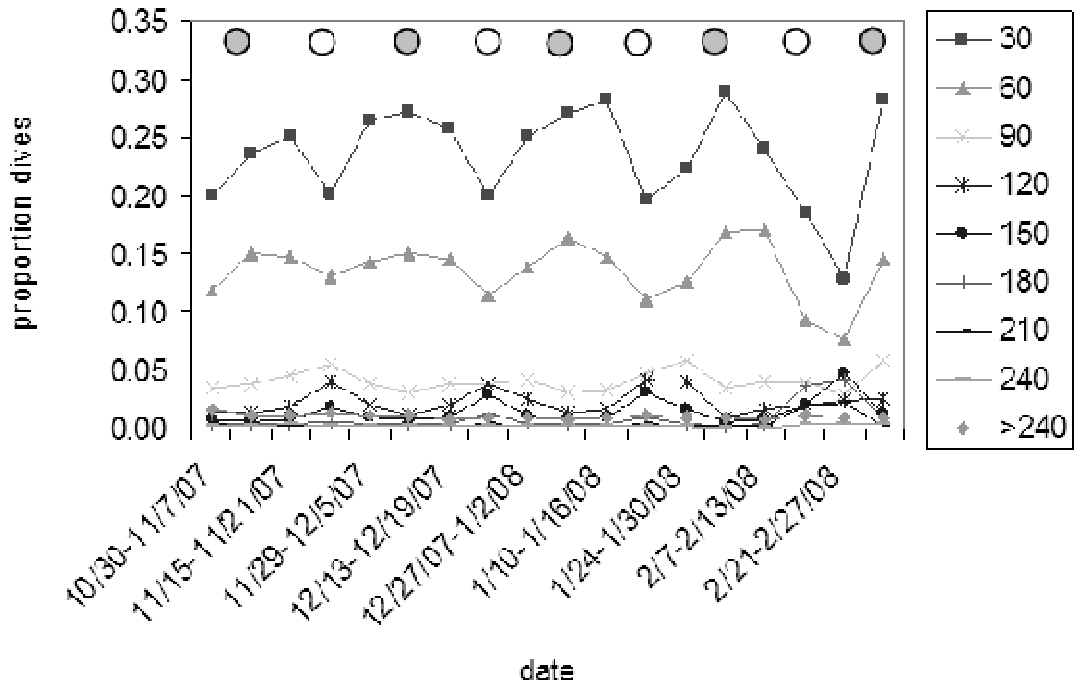

Fig. 6. Average proportion of all dives in each duration range (seconds) during the study period. Proportion of dives ≤ 15 seconds are not shown. Shaded circles represent new moon stage, and open circles represent full moon stages.

Table 5. Average daily proportion of dives lasting various durations (sec). Pups reports the number of pups used to calculate the mean proportion of dives each week. Bold indicates a significant change ($p < 0.05$) for a particular dive duration bin from the previous week.

Week/ date	15	30	60	90	120	150	180	210	240	>240	Pups
1. 10/30-11/7/07	0.4990	0.2723	0.1807	0.0321	0.0066	0.0025	0.0018	0.0007	0.0005	0.0039	34
2. 11/8-14/07	**0.5239**	**0.2503**	**0.1476**	**0.0363**	**0.0202**	**0.0099**	**0.0026**	**0.0011**	**0.0007**	**0.0074**	33
3. 11/15-11/21/07	0.5243	**0.2469**	0.1456	0.0362	0.0231	**0.0115**	**0.0030**	**0.0009**	**0.0006**	0.0078	31
4. 11/22-11/28/07	0.5227	**0.2547**	0.1440	**0.0344**	**0.0212**	0.0109	**0.0026**	**0.0008**	**0.0006**	0.0080	30
5. 11/29-12/5/07	0.5238	0.2563	0.1477	**0.0329**	**0.0171**	0.0091	0.0025	0.0009	0.0006	0.0092	28
6. 12/6-12/12/07	0.5485	0.2801	0.1765	0.0690	0.0180	0.0098	0.0026	0.0009	**0.0006**	**0.0066**	26
7. 12/13-12/19/07	0.5239	0.2544	0.1473	0.0347	**0.0197**	0.0109	0.0027	0.0009	0.0006	**0.0049**	25
8. 12/20-12/26/07	0.5200	0.2554	0.1473	0.0350	0.0213	0.0120	0.0030	0.0009	0.0006	0.0044	25
9. 12/27/07-1/2/08	0.5250	0.2506	0.1437	0.0354	0.0228	0.0134	0.0033	0.0009	0.0006	0.0043	23
10. 1/3-1/9/08	0.5339	0.2446	0.1354	0.0356	0.0250	0.0163	0.0040	0.0009	0.0006	0.0037	23
11. 1/10-1/16/08	0.5547	0.2372	0.1223	**0.0321**	0.0252	0.0193	0.0049	0.0008	0.0004	0.0030	23
12. 1/17-1/23/08	0.5787	0.2322	0.1200	0.0284	0.0182	0.0153	0.0041	0.0007	0.0003	0.0020	21
13. 1/24-1/30/08	0.5962	0.2341	0.1179	0.0274	0.0125	0.0082	0.0022	0.0004	0.0002	0.0008	12
14. 1/31-2/6/08	0.5331	0.2640	0.1506	0.0333	0.0124	0.0042	0.0009	0.0004	0.0002	0.0009	6
15. 2/7-2/13/08	0.5423	0.2653	0.1382	0.0318	0.0131	0.0058	0.0013	0.0008	0.0003	0.0011	4
16. 2/14-2/20/08	0.5731	0.2480	0.1283	0.0297	0.0135	0.0047	0.0009	0.0005	0.0003	0.0011	2
17. 2/21-2/27/08	0.4556	0.2809	0.1776	0.0483	0.0233	0.0093	0.0015	0.0010	0.0005	0.0022	1
18. 2/28-4/3/08	0.4614	0.2891	0.1764	0.0470	0.0150	0.0063	0.0018	0.0008	0.0004	0.0017	1

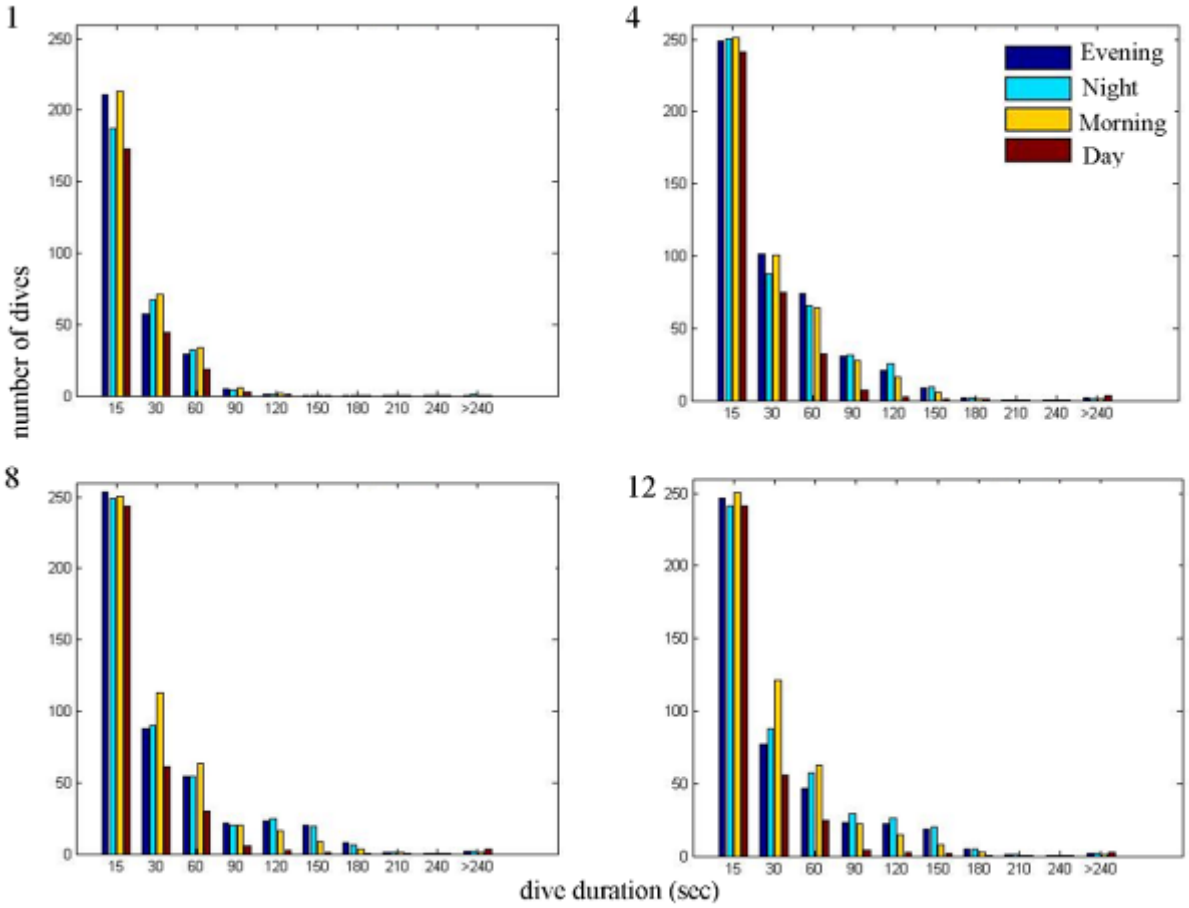

Fig. 7. Effect of time of day on frequency of dive duration in week 1, 4, 8 and 12 (numbers in top left corner of graph), indicating the number of weeks since October 30, 2007. The number of dives is the average across all pups transmitting data, of the mean number of dives in each dive duration bin during that week (N = 29 for week 1, N = 27 for week 4, N = 23 for week 8, N = 14 for week 12). See Table 5 for dates included for each week.

Early in the migratory period, (weeks 1-2) there was little difference due to time of day in the frequency distribution of dive durations (Figure 4). Between November 1 to November 30, 2007, average dive durations were significantly shorter during the day (mean = 15 sec, SD = 7.9, SE = 0.26, N = 907) ($p < 0.0001$), compared to evening (mean = 21.4 sec, SD = 10.3, SE = 0.37, N = 761), night (21.7, SD = 11.1, SE = 0.43, N = 659) and morning (mean = 20.8 sec, SD = 10.32, SE = 0.32, N = 1045) dives.

Average dive durations continued to increase during the first 7 weeks of the migration period. During the month of January 2008 the longest dive durations were still recorded during evening and night, while dive durations during the morning hours decreased. The estimated average dive durations were not significantly different ($p = 0.616$) between evening (mean = 25.9 sec, SD = 6.7, SE = 0.33, N = 422) and night (mean = 26.5 sec, SD = 8.1 ,SE = 0.4, N = 400), while significantly shorter dives were recorded during the morning (mean = 23.3 sec, SD = 6.0, SE = 0.26, N = 534) and day hours (mean = 14.8 sec, SD = 5.23, SE = 0.25, N = 450) ($p < 0.0001$).

Dive Depths

The estimated average dive depths for males (5.7 m, SD = 3.58) was similar, but significantly greater than for females (4.6 m, SD = 2.76) (Mann-Whitney U = 5921760, $p < 0.0001$, N = 7954).

An increase in dive depths was observed over time, and the proportion of dives < 2 m decreased over time (Fig. 8). During the first week, most dives were between 1 to 5 m with no dives > 35 m. The first dives between 35 to 50 m occurred in week 3, and the first dives between 50 to 75 m occurred in week 4 (Table 6). Over half the pups stopped transmitting dive depth data after January 9, 2008, which was one week before half the pups stopped transmitting dive duration data. Similar to the dive duration data, there was an oscillation during which the proportion of dives > 10 m increased during full moons, but the proportion of dives between 5 to 10 m decreased during full moons. Shallow dives (< 5 m) did not show any changes with lunar phases.

The focal dive depths showed a marginally dominant depth bin during the day (1000 – 1600) during November ($F = 0.47$, dominant depth = 0 to 2 m), December ($F = 0.47$, dominant depth = 2 to 5 m) and January ($F = 0.46$, dominant depth = 2 to 5 m). No dominant depth bin was observed during February for any of the 6-hour time periods ($F < 0.39$), or during morning, evening or night in November ($F < 0.3$), December ($F < 0.3$) or January ($F < 0.31$).

Table 6. Average daily proportion of dives at different depths (m). Pups reports the number of pups used to calculate the mean proportion of dives each week. Bold indicates a significant change ($p < 0.05$) for a particular dive depth bin from the previous week.

Week/ date	2	5	10	20	35	50	75	100	125	>125	Pups
1. 10/30-11/7/07	0.271	0.535	0.185	0.009	0.001	0.000	0.000	0.000	0.000	0.000	34.000
2. 11/8-14/07	**0.007**	**0.624**	**0.317**	**0.040**	**0.011**	**0.001**	**0.000**	0.000	0.000	0.000	32.000
3. 11/15-21/07	**0.002**	**0.662**	**0.188**	**0.088**	**0.051**	**0.009**	**0.001**	0.000	0.000	0.000	31.000
4. 11/22-28/07	**0.000**	0.671	**0.157**	**0.100**	**0.064**	0.007	0.000	0.000	0.000	0.000	30.000
5. 11/29-12/5/07	0.000	**0.604**	**0.281**	**0.084**	**0.024**	**0.003**	**0.004**	0.000	0.000	0.000	27.000
6. 12/6-12/07	0.000	**0.694**	**0.237**	**0.044**	0.017	0.004	0.005	0.000	0.000	0.000	26.000
7. 12/13-19/07	0.000	**0.744**	**0.184**	0.040	0.021	0.005	0.006	0.000	0.000	0.000	25.000
8. 12/20-26/07	0.000	0.748	0.177	0.047	0.022	0.005	0.000	0.000	0.000	0.000	25.000
9. 12/27/07-1/2/08	0.000	**0.686**	**0.237**	0.055	**0.018**	0.004	0.000	0.000	0.000	0.000	23.000
10. 1/3-9/08	0.010	**0.636**	0.257	0.064	0.021	0.009	0.003	0.000	0.000	0.000	23.000
11. 1/10-16/08	0.128	0.555	0.212	0.066	0.023	0.010	0.005	0.000	0.000	0.000	23.000
12. 1/17- 23/08	0.249	0.505	0.160	0.043	0.025	0.013	0.005	0.000	0.000	0.000	21.000
13. 1/24-30/08	0.321	0.501	0.100	0.041	0.022	0.010	0.004	0.000	0.000	0.000	12.000
14. 1/31-2/6/08	0.107	0.562	0.174	0.106	0.033	0.011	0.006	0.000	0.000	0.000	5.000
15. 2/7-2/13/08	0.190	0.434	0.278	0.077	0.014	0.006	0.001	0.000	0.000	0.000	4.000
16. 2/14-2/20/08	0.285	0.518	0.119	0.039	0.035	0.003	0.000	0.000	0.000	0.000	2.000
17. 2/21-2/27/08	0.000	0.437	0.331	0.202	0.018	0.010	0.003	0.000	0.000	0.000	1.000
18. 2/28-3/4/08	0.000	0.486	0.335	0.164	0.008	0.005	0.001	0.000	0.000	0.000	1.000

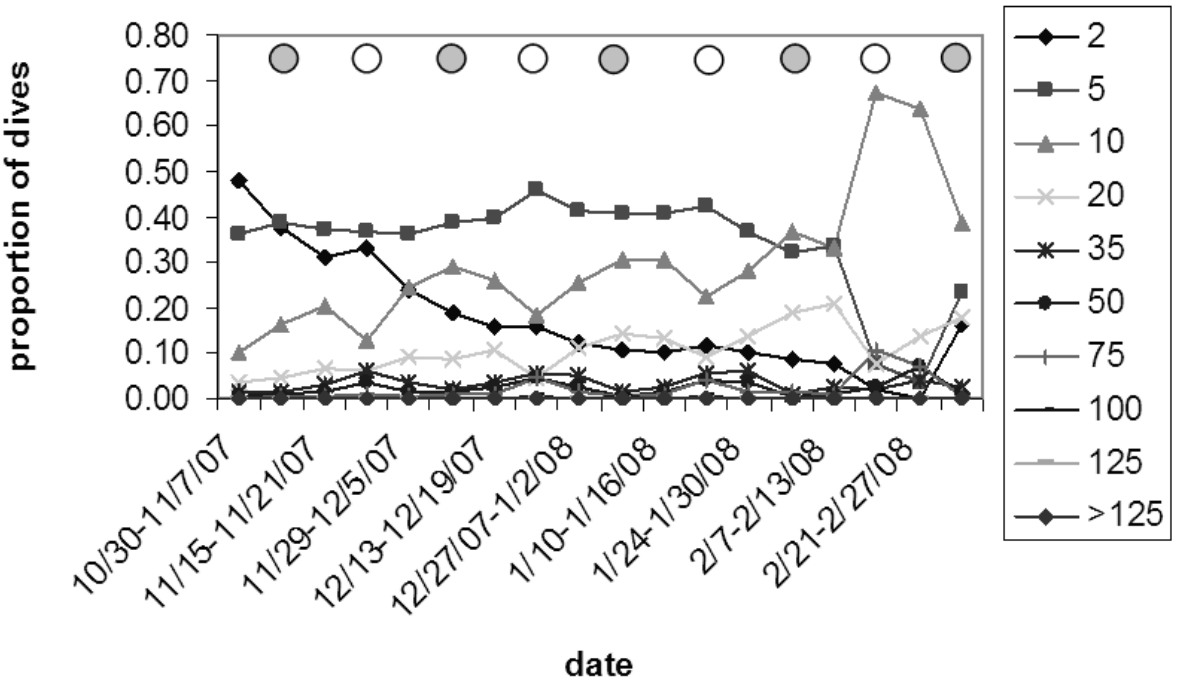

Fig. 8. Average daily proportion of dives at different depths (m) over time. Shaded circles represent new moon stage, and open circles represent full moon stages.

Most of the dives during the day were < 10 m, whereas dives that were > 20 m mostly occurred between evening and morning (Fig. 9). The estimated average dive depths in November were significantly different between time periods ($p < 0.001$, $F = 18.7$, $df = 3$). The Games-Howell post-hoc test showed that dive depths were not significantly different between evening (mean = 5 m, SD = 2.64, SE = 0.09, N = 34), night (mean = 5.38 m, SD = 3.0, SE = 0.12 , N = 34) and morning (mean = 4.78 m, SD = 2.24. SE = 0.76, N = 34) (night vs evening $p = 0.053$, evening vs morning $p = 0.229$), but significantly shallower dives were observed during the day (mean = 2.85 m, SD = 1.23, SE = 0.04 N = 34) ($p < 0.0001$).

By January, pups were still diving significantly deeper during the evening (mean = 8 m, SD = 2.3, SE = 0.48, N = 23), night (mean = 8.4 m, SD = 2.2, SE = 0.46, N = 23) and morning (mean = 7.3 m, SD = 1.7, SE = 0.36, N = 23) compared to day (mean = 4.5 m, SD =1.5, SE =0.31, N = 23) ($F = 18.25$, $df = 3$, $p < 0.001$).

Individual Diving Strategies

All individuals showed a trend of deeper diving over time. The majority of dives from 1 to 2 m occurred during the first 35 days when the overall number of dives also increased (Fig. 9). Generally, the longer the period of shallow diving (1 to 2 m) was, the longer an individual took to reach maximum depths of 75 m. Eleven out of 34 pups recorded at least one dive ranging from 75 to 100 m, but dives > 75 m made up only 0.001% of the total dives recorded (N = 3,360,546). Individuals also showed differences in preferred dive depths over time (Fig. 10). Some individuals showed periods of deep diving ($\geq$ 35 m) interspersed between periods of relatively shallow diving, whereas others preferred to dive to $\leq$ 20 m consistently. During periods of deep diving ($\geq$ 35 m), daily travel speeds did not decrease, but in some cases there were more frequent changes in the direction of travel (Fig. 11). There was no relationship between the frequency of diving behavior recorded and directional swimming (i.e., least changes in direction and relatively high travel speeds).

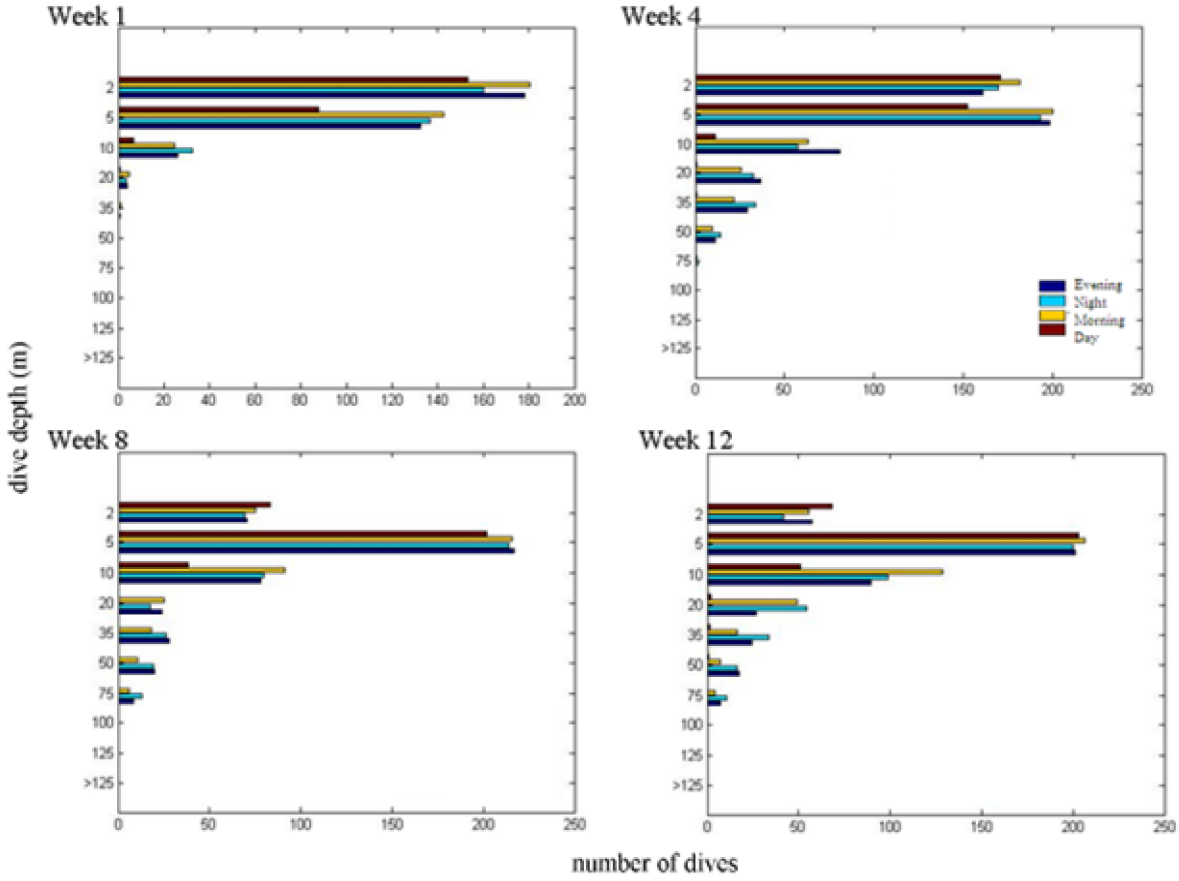

Fig. 9. Effect of time of day on dive depths from weeks 1 to 12. The number of dives is the average number of dives for all pups (N = 29 week 1, N = 27 week 4, N =23 week 8, N = 14 week 12) transmitting data. See Table 6 for dates included for each week.

Nine pups were omitted from the cluster analysis because they transmitted data for less than 2 months, or had gaps (missing data) in their dive records. The analysis showed that pup diving behavior could be grouped into 2 diving strategies based on the proportion of dives at each depth bin and 6-hr time period (Table 7, Table 8). Strategy 1 was strongly diurnal with no dives > 5 m during the day and deep dives occurring during

the evening, night and morning. Strategy 2 also consisted of deep dives between evening and morning, but was characterized by deeper dives during the day as well (Table 7). For simplicity, pups with predominantly strategy 2 behavior will be referred to as deep divers, and pups with predominantly strategy 1 will be referred to as shallow divers, even though both groups exhibit deep dives during the night, evening and morning hours.

Five pups showed only strategy 1 behavior, but no pups showed only strategy 2 behavior. However four pups showed > 85 % strategy 2 behavior, with the complement proportion of strategy 1 behavior occurring earlier in the migration period (i.e., during the month of November), when pups were still increasing their dive depths. Seven pups showed 55 to 80% strategy 2 behavior, 1 pup showed > 55 % strategy 1 behavior, and 9 pups showed a mixed strategy (50% strategy 2, and 50% strategy 1). Most of the individuals classified under the mixed strategy showed mostly the shallow diving strategy 1 behavior, or only a very weak deep diving behavior (Fig. 10).

The mean estimated number of dives recorded in a six-hour period was significantly different between shallow (N = 1427 samples) and deep divers (N = 3048 samples). Deep divers had significantly less dives (mean = 434.5, SD = 149.96) than shallow divers (mean = 451.2, SD = 175.3) (Mann-Whitney U = 1956083, $p < 0.0001$). The difference in the estimated number of dives between shallow and deep divers may actually be greater than the results suggest because of the high likelihood of underestimating the number of shallow dives using histogram data. The mean dive depth for shallow divers was 3.56 ± 0.33 m, for deep divers was 6.36 ± 1.21 m, and for mixed

divers was 4.8 ± 0.86 m. A summary of all individual diving behavior is given in Table 8.

Table 7. Proportion of dives at various depths and times of day for the two dive strategies.

Cluster	Depth	Mean	SD	Evening	Night	Morning	Day
1				0.18	0.17	0.2	0.45
	2	0.408	0.228				
	5	0.458	0.246				
	10	0.095	0.091				
	20	0.024	0.025				
	35	0.011	0.013				
	50	0.003	0.005				
	75	0	0.001				
2				0.32	0.33	0.3	0.04
	2	0.068	0.11				
	5	0.447	0.158				
	10	0.322	0.162				
	20	0.114	0.079				
	35	0.03	0.02				
	50	0.013	0.014				
	75	0.005	0.008				

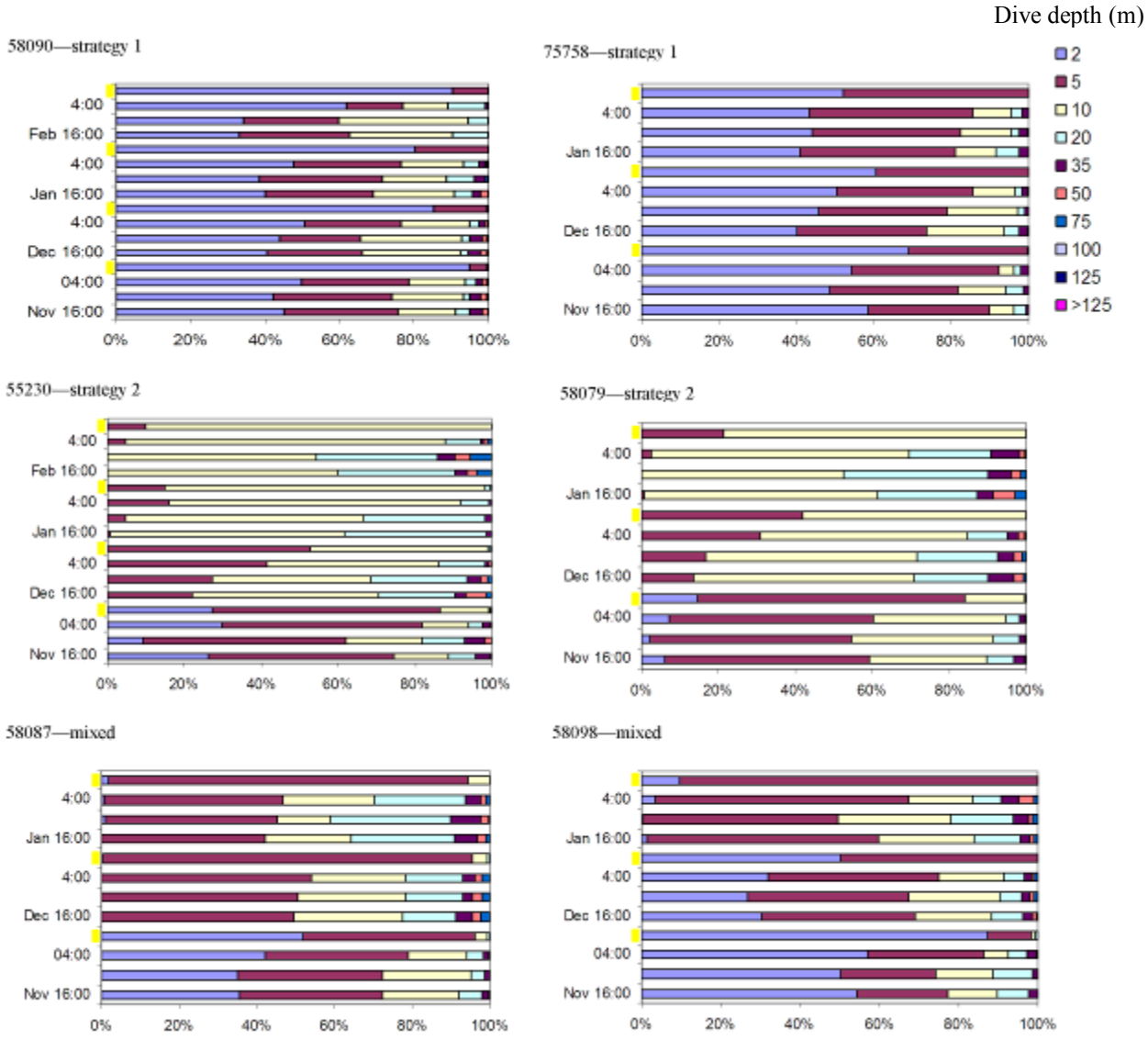

Fig. 10. Individual dive behavior by time of day showing strategies 1, 2 and mixed (50% strategy 1, 50% strategy 2). Yellow bars on the y-axis denote daytime hours. Colored bars are depth bins.

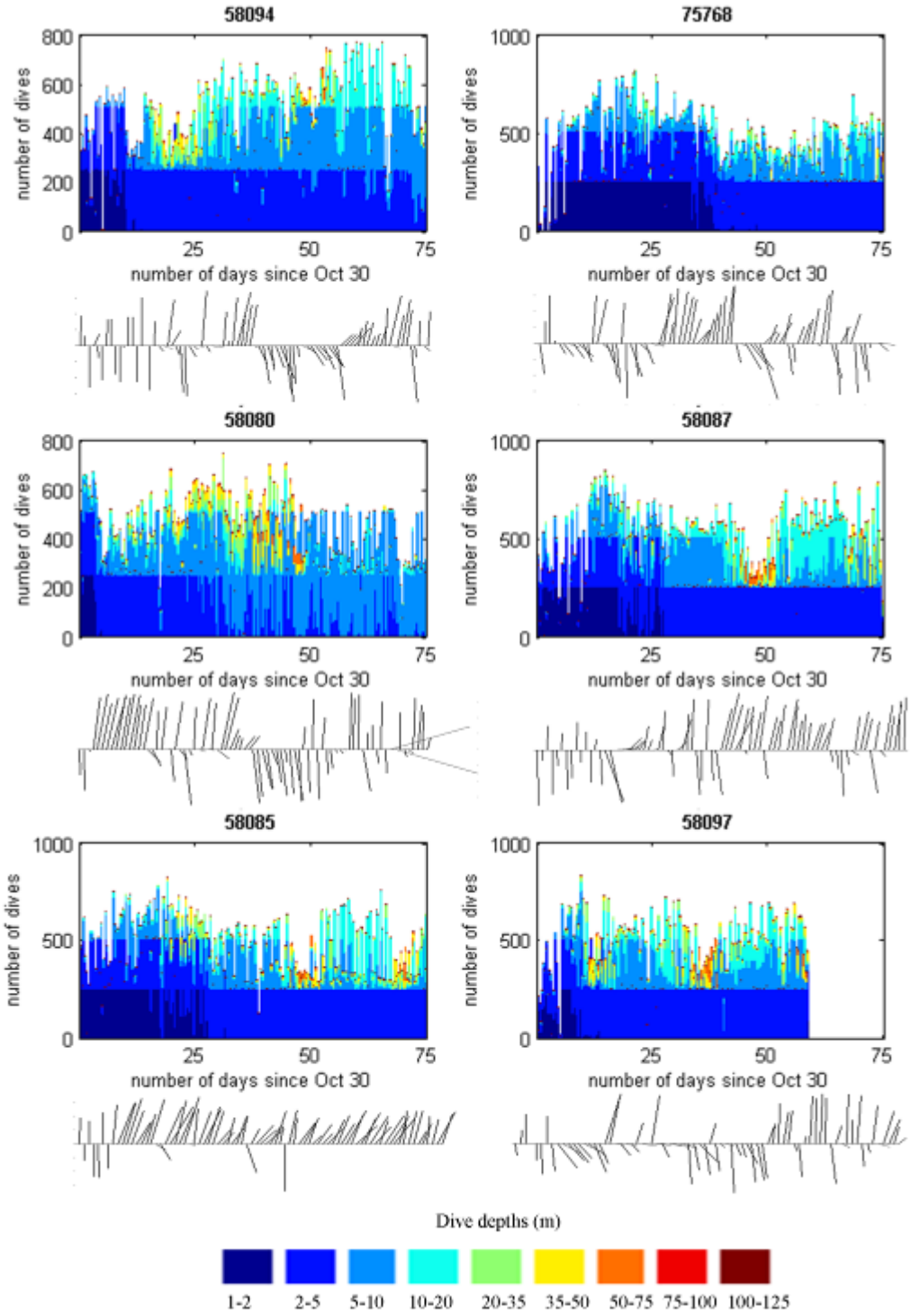

Fig. 11. Individual dive depths and velocity vectors for six pups. Vector lengths indicate speed, and angles indicate bearing from previous location (north is up).

Table 8. Summary of individual dive behavior. Days to max depth were only calculated for individuals that dove at least 50 m. Max depth reported is the upper limit of the deepest histogram bin in which a dive was recorded.

ID	Sex	% Strategy 1	% Strategy 2	Mean dive depth (m)	SD depth	Max depth (m)	Days to max depth	Mean dive duration (sec)	SD duration
55031	Female	33	67	5.3	3.23	75	19	24.8	10.5
55230	Male	12.5	87.5	8.3	4.01	100	40	26.2	11.2
55231	Male	-	-	1.7	0.26	10	-	10	5.1
58079	Female	8.3	91.7	7.7	3.76	100	30	24.2	7.1
58080	Male	8.3	91.7	7.5	3.94	100	29	26.2	7.3
58083	Male	-	-	2.4	0.82	50	-	16.2	10.2
58084	Male	-	-	4.9	2.22	20	-	79.8	74.7
58085	Male	50	50	5.8	3.21	75	20	22.4	8
58086	Female	-	-	2.9	1	35	-	12.7	4.3
58087	Male	50	50	6.3	3.8	100	49	24.3	10.5
58088	Male	-	-	2.3	0.51	20	-	13.6	4.9
58089	Male	-	-	1.8	0.22	10	-	21.4	42.6
58090	Female	100	0	4	2.13	100	83	20.1	13.5
58091	Female	50	50	5.4	2.92	100	83	23.7	9.9
58092	Female	100	0	3.4	2.1	75	20	17	6.7
58093	Female	-	-	3.9	2.1	75	12	19.7	7.9
58094	Male	33	67	6.2	2.9	75	19	21.2	7.1
58095	Female	58.3	41.7	3.8	2.1	75	24	19.3	8.3
58096	Male	87.5	12.5	3.2	2.2	100	50	21.1	8
58097	Male	33	67	6.9	4.1	75	24	24.4	7.7
58098	Male	50	50	4.6	3	100	84	20.7	14.4
58099	Female	43.8	56.3	4.9	2.3	75	29	22.6	7.4
58100	Female	100	0	3.7	1.8	75	25	22.1	9.5
58101	Female	-	-	2.5	0.98	50	18	13	8.4
74801	Female	50	50	4.4	2.6	75	22	23.1	16.9
74802	Male	50	50	3.7	1.9	75	44	21.2	8.6
74803	Female	-	-	3.6	1.9	75	23	19.9	9.6
74804	Female	25	75	5.6	1.5	75	24	21.4	7

Table 8. continued

ID	Sex	% Strategy 1	% Strategy 2	Mean dive depth (m)	SD depth	Max depth (m)	Days to max depth	Mean dive duration (sec)	SD duration
74805	Male	50	50	4.2	2.6	100	57	20	8.4
75758	Female	100	-	3.1	1.76	75	31	20.4	7.3
75759	Male	25	75	6.3	2.8	100	81	26.6	11.3
75768	Female	50	50	4.1	2.1	75	37	20.6	6.9
75769	Female	43.8	56.3	4.9	3.1	100	53	22.5	16.4
75770	Male	100	-	3.7	2.2	75	24	25.8	12.3
75771	Female	50	50	4.8	2.7	75	54	22.7	8.8

Discussion

Northern fur seal pups from Bering Island showed a trend of increasing diving capability as they matured during the first few months as sea. Although the frequency of deeper dives increased over time, no dives > 100 m were recorded, which is well below the range of maximum recorded dive depth (175 – 200 m) for adult females and juvenile males (Gentry 1986, Sterling & Ream 2004). The maximum dive depth in BI pups was > 75 m, in contrast to < 75 m for Pribilof Islands (PI) pups. Significantly deeper dives were observed in male pups compared to female pups in this study, but the difference in mean dive depths between the sexes was only 1.1 m. This could be an artifact of overfilling the shallow depth bins (< 5 m) and recording smaller numbers of dives for males. Current literature does not provide evidence for deeper diving in male pups. Maturation also was observed for dive duration, which increased within the first 3 weeks of the migration period, suggesting that animals were improving their diving ability.

Another measure of maturation of diving skills was the elapsed time to reach maximum recorded dive depth of 75 m, which occurred within 25 – 30 days for both BI and PI pups. Although uncommon, some BI pups dove > 20 m during their first week of migration. BI pups did not consistently dive deeper than 20 m until at least 2 weeks into the migration period. Baker (2007) reported similar precocial deep diving behavior in most pups from the PI, but some individuals in his study started diving consistently deeper than 20 m over a shorter period of time (within 5 days of the start of their migration). The bathymetry that pups from both populations encounter during their first two weeks of migration far exceeds their maximum dive depths, and it is unlikely that

encountering deeper water played a major role in the earlier onset of deep diving in PI pups.

Diurnal (shallow daytime) diving behavior by BI pups was similar to that for migratory PI pups. Once pups began their migration, the early predominance of shallow, daytime dives transitioned into deeper dives during the evening, night and morning hours. The increased frequencies of night and evening time dives by BI pups were similar to those for both adult females and pups from the PI (Baker 2007, Lea et al. 2006).

As compared to pups from the PI, BI Pups also appeared to make more shallow dives during the first 20 days of their migration. At least 25% of BI pup dives were 2 to 5 m deep during the first 20 days of migration, whereas PI pups generally spent less than 25 % of their time at 2 to 5 m during their first 20 days at sea. After 20 days, most pups in this study continued to conduct at least 25% of their dives in shallow water throughout the day. The daytime diving behavior of pups from BI was also slightly different from what was recorded in the PI. Individuals in this study were recorded diving up to 10 m during the day, whereas pups from the PI had almost no dives over 5 m during the day (Lea et al 2006). Pups from the PI also showed a decrease in daytime diving over time (Lea et al 2009b), whereas BI pups using the deep-diving strategy conducted more deep dives during the day over time.

These results suggest that some BI pups tend to make more deep dives during the daytime hours, and more shallow dives (2 to 5 m) in the night, evening and morning hours as compared to PI pups. Increased dive effort (number of dives per day) was also

observed in BI pups, but because of the higher proportion of shallow dives throughout a 24-hour period, the mean dive depths were generally shallower in BI pups (83% dives less than 10 m), than for PI pups (77% dives less than 10 m). The prevalence of the deep dives (> 10 m) occurring during the evening, night and morning suggests that pups from BI and PI forage on vertically migrating prey that are not available during the daytime hours.

Adult females from the nearby Medny Island (of the Commander Islands) displayed more shallow dives (< 20 m) compared to adult females from St. George Island (of the Pribilof Islands) (Gentry 1998). Medny Island females spent significantly more time at this depth (*ca.* 20 m), and frequently made shallow dives throughout the day, as did the deep diving pups in BI (this study). The overall pattern of deeper nocturnal diving was still observed in Medny and St George females, but St. George females made deeper dives that were less frequent, and had fewer dives during the day compared to Medny Island females. Gentry (1998) hypothesized that females from Medny Island were visiting a warm water region at 20 m that suggested that animals were utilizing a prey resource that is not used by pups or adults from the PI.

The increased daytime diving behavior in BI pups suggest either: 1) increased foraging behavior that occurs during the day, 2) greater directional traveling at depths greater than 2 m during the day. If increased foraging during the day occurs, pups would be foraging on prey found in shallow water (< 10 m). This depth range is slightly shallower than the depths frequented by females from Medny Island, and much shallower than the dive depths of adults that are considered deep divers (> 70 m).

However, deep diving BI pups could be showing the start of deep diving behavior that occurs throughout the day in adults.

Sterling & Ream (2004) found that juvenile males from the PI showed mostly shallow diving off-shelf, and deeper diving in on-shelf regions. Deeper on-shelf diving was thought to be related to foraging on juvenile walleye pollock (*Theragra chalcogramma*) that vertically migrate in the same diurnal pattern (Schatbetsberger et al. 2000) observed in northern fur seals. Adult female northern fur seals were also observed conducting fewer dives in deep water when foraging on pollock (Goebel et al. 1991).

Increased feeding on juvenile fish could be driving the deeper daytime diving behavior in pups. Juvenile walleye pollock generally migrate vertically into deeper water during the day, but in some regions in the eastern Bering Sea, juvenile pollock did not migrate, rather they stayed within 10 to 12 m of the surface where zooplankton abundance was higher (Bailey 1989). The higher occurrences of eddies in the Kamchatka strait compared to the Alaskan stream (Stabeno et al. 1994) could promote higher zooplankton concentrations in the surface waters during the day in the western Pacific, which allows more juvenile pollock to stay near the surface during the day and subsequently allows BI pups to take advantage of this resource.

Rookery specific differences in diet (Sinclair et al. 1994, Antonelis et al. 1997, Robson et al. 2004, Zeppelin & Ream 2006) complicates the interpretation of the importance of pollock in northern fur seal diets. Moreover, diet studies of these seals rely on data obtained from adults and not pups. If the shallow diving BI pups are consuming mostly pollock, it is contrary to the observed diet of adults from the

northwest rookery of BI. Adults from the northwest rookery (where pups from this study were tagged) have not been observed to consume large amounts of pollock, whereas adults from the nearby north rookery on BI have consumed higher quantities of pollock (Blokhin 2006) in the last six years. The lack of information on the diets of pups from the various rookeries requires us to speculate that some differences in the diving behavior of pups from BI and the PI are related to differences in preferred prey.

Individual differences in diving strategies were identified by the cluster analysis; 16 out of 26 pups had at least 50 % of their diving behavior characterized as strategy 2 (i.e., deeper divers with high frequencies of deep dives during the day). Only 10 pups showed a predominance (> 60%) of night, evening and morning diving behavior, as displayed by PI pups. The deeper daytime dives were mostly associated with the deep diving pups, therefore any increase in foraging behavior throughout the day is likely associated with only this subgroup of BI pups.

The deep divers among BI pups behaved similarly to juveniles from the PI whose deep dives were related mostly to foraging on the continental shelf. The predominantly deep divers in this study were closer to the shelf margin, whereas only one out of sixteen BI pups that were shallow divers were located near the continental shelf (Fig. 12). As the migratory period progressed, fewer animals were observed close to the continental shelf, thus increasing the occurrence of strategy 1 diving (i.e., more mixed diving pups were classified as shallow diving) as more individuals entered deeper water. A more detailed analysis of pup behavior and bathymetry is discussed in Chapter VI.

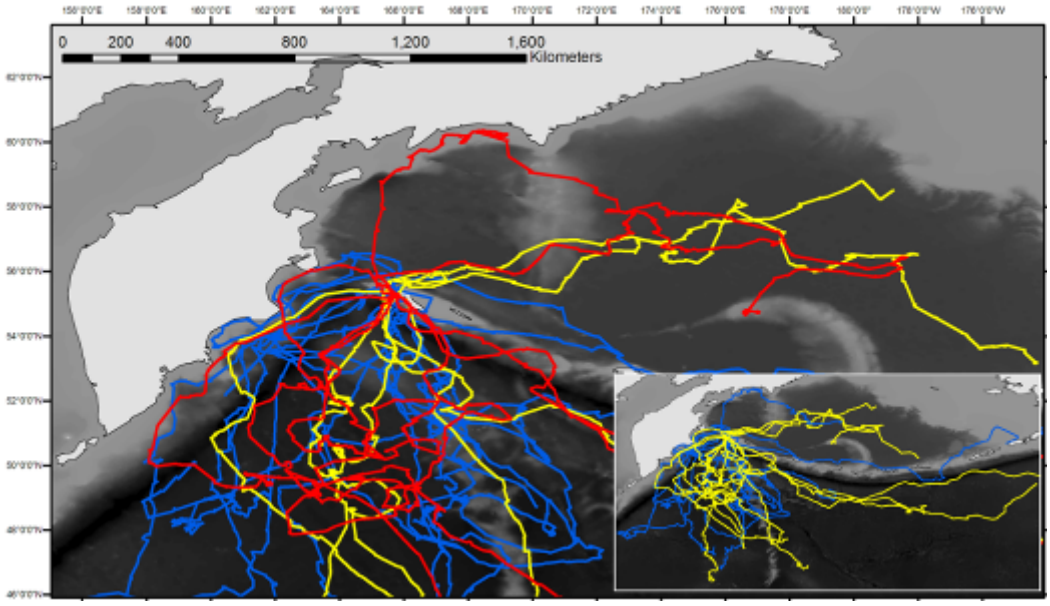

Fig. 12. Close-up of pup locations showing predominantly deep divers (blue), predominantly shallow divers (yellow) and mixed divers (red) over bathymetry (lighter grey areas indicate shallower water). Inset shows the mixed diving pups reclassified as either shallow (if 50% strategy 1) or deep (if 50 to 55% strategy 2) divers.

Studies on diving behavior and foraging energetics suggest that there are differences in the metabolic costs of different diving strategies (Costa 1988). Higher mass gain was observed in deep diving adult females (Goebel et al. 1991), and on-shelf diving (equivalent to deep diving pups) juvenile males (Sterling & Ream 2004). It is possible that a slight difference in mass gain between deep or shallow divers could be important to pups, which have elevated metabolic rates (Costa & Gentry 1986, Donohue et al. 2000), but more research is needed to determine whether the deep diving strategy is more efficient, and therefore advantageous to pups.

The relatively shallower daytime diving of the 'deep diving' pups, when compared to adults and juveniles, suggests that they are unlikely to be foraging on benthic prey that occur at depths of over 75 m, and therefore, increased daytime foraging may not actually be occurring. An alternative explanation for the daytime diving behavior in some BI pups is that traveling behavior affected their dive records. Increased diving behavior from 2 to 5 m could be recorded as animals swim under large waves, but this is an unlikely explanation for the higher frequencies of daytime dives between 5 to 10 m. The velocity vectors showed few deviations in direction of travel, which would indicate pups were mostly directional swimmers. However, average travel speeds in BI pups (1.35 km h^{-1}) were lower than the reported average travel speeds in PI pups (1.9 km h^{-1}) (Baker 2007). This lack of evidence for increased directional swimming in BI pups compared to PI pups does not support the hypothesis of increased daytime traveling as a major cause of the observed increase in daytime dives.

The slower travel speeds in BI pups also are contrary to an increase in daytime diving behavior, or swimming below the surface, to avoid predators. Observations of killer whale predation on northern fur seals have been documented around the rookeries of the Commander Islands (Mamaev & Burkanov 2006), but there is little support for predation of pups particularly while in the open ocean. This suggests that pup daytime diving behavior is not for predator avoidance.

Conclusions

The trends of increasing dive durations and dive depths over time were similar between PI and BI pups. All pups showed a strong diurnal pattern of more dives between

the evening and morning, and fewer dives during the day. Dives were also deeper during full moon phases compared to new moon phases. The daytime deep-diving strategy in BI pups was not identified early in the migration period for PI pups. Although the deep-diving strategy was related mostly to on-shelf locations early in the migration period, individuals that were deep divers continued this strategy later on, even after moving into deeper water. The daytime dive depths of deep-diving pups were much shallower than the maximum observed dive depths of the same individuals at night, and also shallower than the depths of most benthic prey species. Thus, deep diving during the day may not be related to foraging behavior, and further investigation of BI pup foraging is discussed in Chapter IV.

CHAPTER IV

FORAGING BEHAVIOR OF NORTHERN FUR SEAL (*Callorhinus ursinus*) PUPS USING STOMACH TEMPERATURE TELEMETRY

Introduction

The feeding behavior of wide-ranging marine predators is difficult to observe. Most studies rely on satellite telemetry to track the movements and record dive behavior of individuals, and feeding behavior is then inferred from the dive depth, duration and temporal frequency of dives. Time Depth Recorders (TDRs) also allow the shapes of the dive profiles to be identified, and certain dive profiles (e.g., U-shaped dives) combined with swim speeds (Horsburgh et al., 2008) can indicate foraging behavior.

The use of stomach temperature telemeters is advantageous because it can directly measure ingestion events by measuring drops in stomach temperature whenever cold prey items are eaten. Ideally, during a feeding event, there is a sharp drop in stomach temperature with a slow recovery to normal body temperature (Kuhn and Costa 2006, Austin et al. 2006). However, animals are also known to ingest sea-water (a process known as mariposa) which will also result in a sharp drop in stomach temperature. These events can be identified from stomach temperature records because water ingestion typically has a very short recovery time for stomach temperature to return to normal body temperature (Gales & Renouf 1993, Andrews 1998). Thus, the use of satellite-linked stomach temperature telemetry allows more direct identification of when, and where feeding behavior occurs.

The purpose of this study was to identify when feeding events occurred in northern fur seal (*Callorhinus ursinus*) pups that could then also be used in combination with location data to determine approximately where feeding behavior was concentrated. Northern fur seal pups are an ideal species and life stage for testing this technology because they range over a wide area, but very little information is known about the location of important feeding areas within their range.

The occurrence of long feeding events was hypothesized to occur during the night hours as inferred from increased diving events in northern fur seals (Lea 2006, Baker 2007). The use of stomach temperature telemetry in my study would provide greater support for feeding behavior during the night hours, when individuals are thought to feed on vertically migrating prey. Increased daytime feeding by some deeper diving pups was hypothesized as evidence for higher mass gain in a subgroup of Bering Island (BI) pups (Chapter III).

An auxiliary objective of this study was to evaluate the effectiveness of the stomach temperature telemeters and the algorithms that identify ingestion events. Use of stomach temperature telemetry is relatively new, and most individuals do not retain stomach temperature loggers for longer than a week without an additional retention device. Both the type of telemeter, and retention device had never been tested under field conditions before this study, and these results provide important information about the procedures, equipment, and suggested improvements.

Methods

Study Site and Animals

The study site was located on Bering Island, Russia (*ca*. 55.29°N, 165.77°E) where 17 male and 18 female northern fur seal pups were tagged with Mk10-AL satellite-linked time depth recorders (SLTDR, Wildlife Computers, Redmond, WA) that recorded data on at-sea movements, and stomach temperature telemeters (STT) that recorded stomach temperature. The data were the transmitted automatically through ARGOS satellites. A rubber esophogeal tube was used to insert the STT into the stomach of each anesthetized animal. The STTs were tube-shaped (*ca.* 63 mm in length x 21.5 mm in diameter), and encased in epoxy. Each STT was attached to a U-shaped, soft-rubber retention device with string (Fig. 13). Over time, the string detached from the retention device, allowing the animal to regurgitate the STT. The telemeters transmitted data on ingestion events based on stomach temperature to the back-mounted SLTDR, and these data were stored in memory and then transmitted to an Argos satellite, along with data on dive depth and duration, when the animal was at the surface. Animals were tagged in 30 -31 October, 2007 just before they departed their natal rookeries to begin their first winter migration. During this period, pups may remain at sea for over two years before returning to land.

Data

The STT normally recorded stomach temperature (°C) every minute (low resolution mode), but shifted to every 30 seconds (high resolution mode) when triggered by an

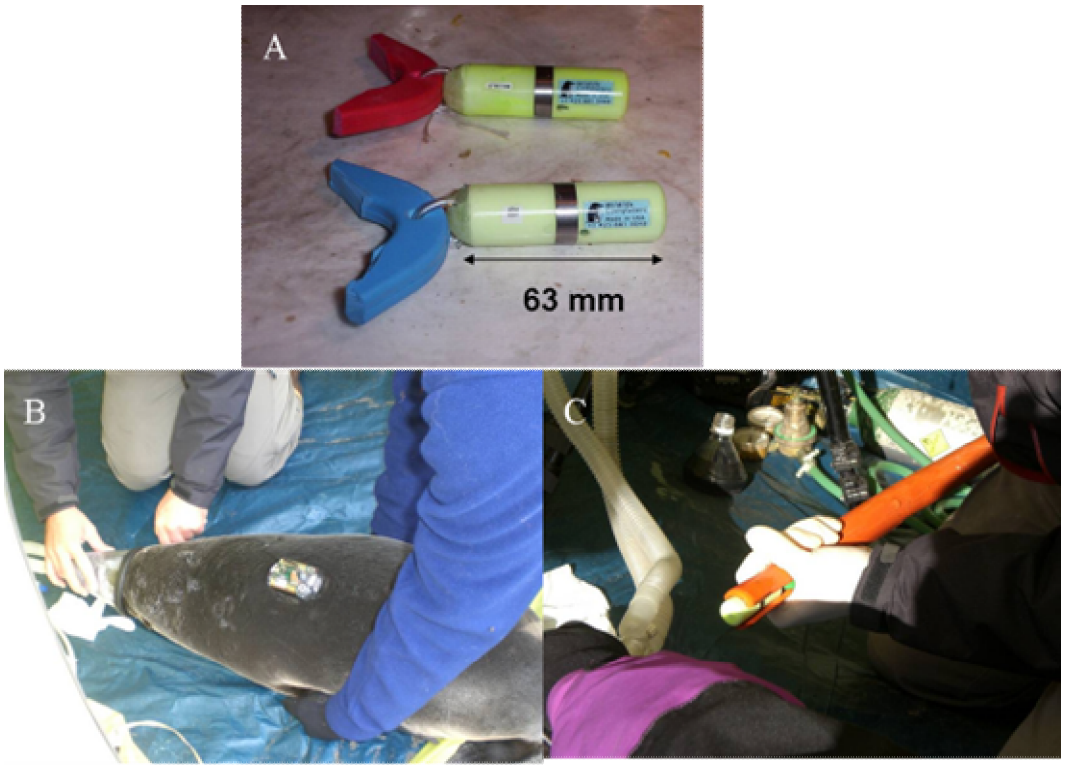

Fig. 13. Procedure for inserting stomach temperature telemeters. (A) Stomach temperature telemeters with retention devices (B) anesthetizing animals and attaching satellite tags and (C) inserting the stomach temperature telemeters using a rubber, esophogeal tube.

ingestion event. Trigger events included one or both of the following: (1) an absolute stomach temperature of 35°C, or (2) rate of stomach temperature drop of 0.5°C min^{-1}. The actual messages received via satellite through Service Argos were first decoded using Wildlife Computers Argos Message Decoder Version 1.0.48, which saves the data as a comma delimited file in Excel. Each record comprised a date and time, PTT (Platform Telemetry Transmitter) number (i.e., a unique identification code for each

animal), a stomach temperature value, status message and, if appropriate, a depth value for the 'feeding deepest depth' status message.

Importing Data

Each status message was assigned a code (Table 9) in Microsoft Access, which could be queried to export records with only PTT number, date, stomach temperature and status value as a text file. Because the date records were truncated during the exporting process (each date was limited to 2 decimal places), TextPad software was used to import the complete date records as a text file.

Table 9. Status and assigned code for each stomach temperature record.

Status	Code
Feeding deepest depth	1
Feeding ends	2
Feeding initial stomach temperature	3
Feeding minimum stomach temperature	4
Feeding second stomach temperature	5
Feeding starts	6
High resolution	7
Low resolution	8
No pill	9

The data were analyzed using MATLAB Ver. 2010a to identify ingestion events, determine STT reliability, filter out water ingestion events, and finally, determine when the longest ingestion events occurred. The dataset for November and December 2007 was expected to include over 1 million records, and therefore a separate script was created to load the data. The date variables were appended to the stomach temperature variables while they shared the same index numbers. The high number of stomach temperature records that needed to be transmitted over satellite caused a number of corrupted messages and regions where no data were available. Gaps in stomach temperature data were assigned the value NaN. Some of the records were not in chronological order in the original decoded file, particularly records related to feeding deepest depths. Therefore, the data were sorted into chronological order before being plotted.

The program was designed to allow the user to visually inspect the data for each seal using the PTT number, and thus to determine whether to include it in the analysis, or discard it if errors were associated with the data source. Additionally, the user could save the variables during discontinuous analysis.

Individual Animal Analysis

Analyses of stomach temperature records for individual pups were conducted after loading the dataset. The script to analyze stomach temperature records utilized a loop to include all 35 animals by sequentially entering the PTT number, or to exit the analysis by entering ‘999’ when the next PTT number was requested. During the loop, the records related to the individual PTT would be identified, and the starting times,

ending times and periods of high resolution were plotted in green, red and blue respectively (Fig. 14) for each individual. The duration of each ingestion event (min) and the total number of ingestion events identified were calculated.

Water ingestion events were first filtered by removing all ingestion events lasting < 5 min (Fig.14). The mean duration of actual feeding events was then calculated after removing mariposa events. For each animal, the total number of events, number of filtered (without water ingestion) events, and mean feeding duration was displayed in the workspace to provide even more information on whether the record appeared adequately complete for use in later analysis.

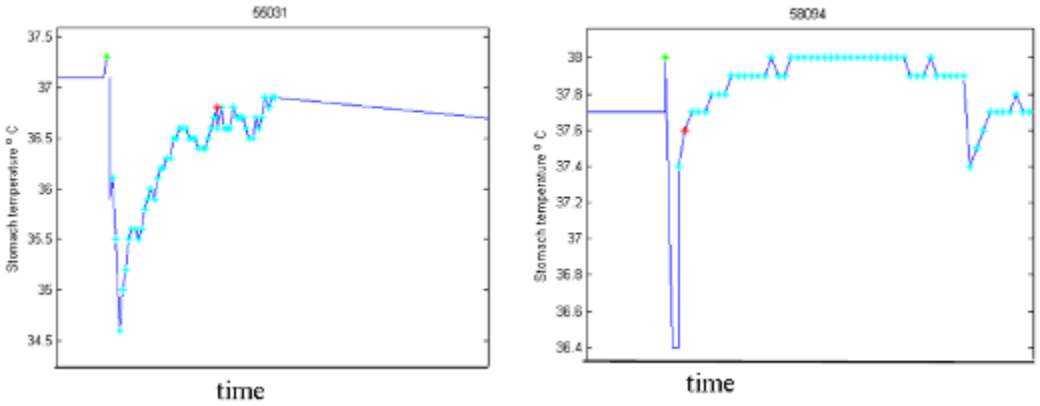

Fig. 14. Stomach temperature records showing the slow recovery of an actual feeding event, and the rapid recovery after an assumed water ingestion event. Green, red and light blue indicate start, end and high resolution status messages respectively.

Timing of Feeding Events

After the individual analyses were completed for all 35 animals, the total number of feeding events, total number of filtered feeding events, and average feeding duration were calculated across all animals (regardless of whether or not their data were to be used in further analysis). To test the hypothesis that most foraging behavior occurred at different times of day for each of the three diving strategies (Chapter III), I plotted the durations of all ingestion events grouped by dive strategy (i.e., deep, shallow and mixed diving strategies).

Diving Strategy Comparisons

Only ingestion events lasting > 5 min were used in the analysis in an attempt to remove the water-ingestion events. The timing of non-water ingestion events were then time-matched to the closest satellite locations of the animal, and then overlaid on images of sea surface height altimetry using ArcGIS 9.2.

The deepest depths reached during an actual ingestion event were compared for each of the three diving strategies identified: deep, shallow and mixed diving (Chapter III). Ingestion event depth records in which the stomach temperature did not fall below 37˚ C were excluded from the analysis. A Kruskal-Wallis test was used to test for significant differences in mean foraging dive depths among the three dive strategies, using the mean dive depths for each individual as replicates.

Location of Ingestion Events

The locations of all ingestion events lasting $\geq$ 20 min were identified using the start time of the ingestion event and the closest available time-matched Argos location.

Ingestion events that differed by more than 12 hours from an Argos location were not included in the analysis. Argos locations were filtered to exclude: travel speeds of > 5 km h^{-1}, turn angles < 25 degrees, and consecutive locations separated by > 1,000 km, using the Satellite Tracking and Analysis Tool (STAT) (Coyne and Godley 2005). Approximate locations for ingestion events were plotted on maps of sea surface height anomalies and geostrophic currents using data obtained from Aviso Altimetry project, and the Maptool function in STAT. Only animals with $\geq$ 3 long ingestion events ($\geq$ 20 min) were used in the analysis.

Results

The program identified 87.8% of all ingestion events, with a mean of 5.4 $\pm$ 7.4 additional events manually identified (without the use of the program) for each individual. The median date for the end of transmissions for all individual pups was 20 November, 2007, with transmissions ranging from 3 to 82 days (mean = 25.8 $\pm$ 21.1 days). Stomach temperature records with gaps > 10 h were excluded from further analysis. Some individuals appeared to cease regular transmissions, but sporadically transmitted a few minutes of data after several days or weeks (Table 10).

Probable water ingestion events (lasting < 5 min) made up 31 % (N = 353) of all ingestion events (N = 1148). The overall mean duration of an ingestion event was 18.36 $\pm$ 24.8 min, whereas the mean duration of probable successful foraging events was 25.36 $\pm$ 27.37 min. The overall mean number of ingestion events per day was 1.4 $\pm$ 0.94

events, whereas this decreased to 0.97 ± 0.71 events per day for probable successful foraging events.

Duration of feeding events was not significantly different among strategies for deep (mean = 18.75 ± 7.1, N = 9), shallow (mean = 23.1 ± 18.3, N =7) and mixed divers (mean = 24.3 ± 10.92, N = 6) (Kruskal-Wallis p = 0.563, Chi-square = 1.15, df = 2). The duration of feeding events also was not significantly different between males (19.29 ± 5.6 min, N = 11) and females (22.04 ± 14.8 min, N = 15) (Mann Whitney U = 73, p = 0.622). Most long feeding events (> 20 min) occurred between 1700 - 0700 local time (–12 UTC), and only mixed and deep divers showed long feeding events during daylight hours (1000 – 1700) (Fig. 15).

The deepest depths reached during an ingestion event were not significantly different (p = 0.322, df = 2, Chi-square = 2.269, df = 2) among deep (mean = 5.22 ± 0.85, N = 10), shallow (mean = 5.28 ± 1.08, N = 7) and mixed (mean = 4.59 ± 0.98, N = 9) divers (Fig. 16). Ingestion events in pups occurred at deeper depths as time increased since leaving the rookery, primarily for shallow and mixed divers (Fig. 17). Foraging depth records for deep divers ended 35 days earlier than the last transmissions for shallow and mixed divers, therefore, any progression to deeper daytime foraging dives in deep diving animals may not have been captured in data of this study.

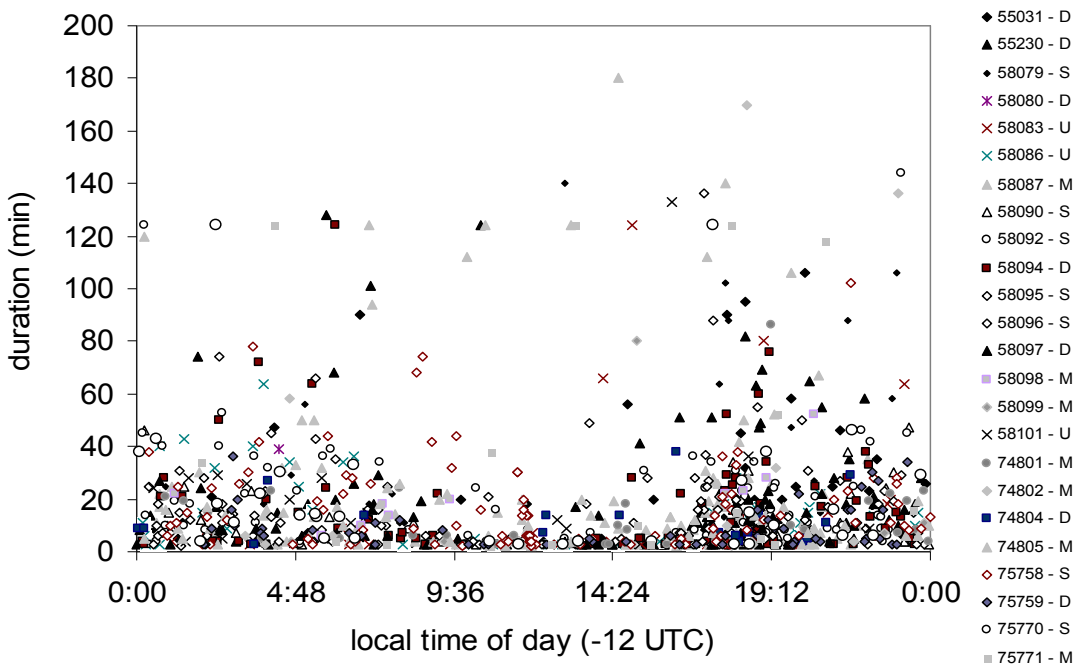

Fig. 15. Time of day and duration of ingestion events. Diving strategies are denoted for all individuals as follows: D = deep diver, S = shallow diver, M = mixed diver, U = unknown.

Table 10. Comparison of MATLAB identified and manually identified ingestion events by individual animal.

PTT	Include record	No. program identified events	Total no. events	MATLAB filtered duration (min)	Mean overall duration (min)	Last transmission	Max gap in record (HH:MM)	Mean no. daily events (> 5 min)
55031	Y	39	44	27.29	24.2 ± 27.3	11/18/2007		1.52
55230	Y	57	71	17.36	21.5 ± 26.9	12/14/2007		1.16
55231	N	0	0	0		11/8/2007		-
58079	Y	32	40	16.67	27.5 ± 33.9	12/11/2007		0.74
58080	Y	1	1	39	39	11/3/2007		0.33
58083	Y	20	24	27.6	19.8 ± 31.2	12/22/2007		0.25
58084	N	1	1	124		12/5/2007		-
58085	N	3	3	124		11/5/2007		-
58086	Y	42	43	20.55	15.9 ± 14.1	11/9/2007		3
58087	Y	77	87	24.69	21.9 ± 33.7	12/12/2007		1.53
58088	N	1	1	0		11/11/2007		-
58089	N	1	1	124		11/4/2007		-
58090	Y	23	56	17.53	14.1 ± 11.9	11/16/2007		2.71
58091	N	4	4	48.66		11/8/2007		-
58092	Y	89	100	24.04	17.2 ± 21.02	1/20/2008		0.94
58093	Y	5	5	7	5.8 ± 1.9	11/7/2007		0.38
58094	Y	65	79	23.28	16.6 ± 20.7	12/2/2007		1.36
58095	Y	93	114	24.38	15 ± 18.5	12/22/2007		1.40

Table 10. continued.

PTT	Include record	No program identified events	Total no. events	MATLAB filtered duration (min)	Mean overall duration (min)	Last transmission	Max gap in record (HH:MM)	Mean no. daily events (> 5 min)
58096	Y	14	11	45.58	16.5 ± 18.1	11/20/2007		0.43
58097	Y	42	50	15.26	14.6 ± 16.5	11/20/2007	9:14	1.67
58098	Y	8	10	19.62	21.5 ± 12.6	11/24/2007		0.40
58099	Y	8	9	9	13.1 ± 25.2	11/10/2007		0.27
58100	Y	7	7	75.17	65 ± 46.6	11/5/2007	1:14	1.00
58101	Y	21	26	16.42	19.5 ± 24.7	11/21/2007		1.05
74801	Y	22	34	12.73	12.4 ± 14.9	11/19/2007	0:52	1.05
74802	Y	10	14	38	31.5 ± 54.2	12/8/2007		0.18
74803	N	0	0	0		11/5/2007		-
74804	Y	15	18	21.55	12.3 ± 9.7	11/10/2007		1.27
74805	Y	55	57	21.89	16.2 ± 23.9	1/13/2008		0.31
75758	Y	76	92	21.26	15.79 ± 17.2	1/10/2008		0.62
75759	Y	43	51	13.28	9.7 ± 8.5	11/24/2007	2:22	1.16
75768	N	2	2	124		11/6/2007		-
75769	Y	7	7	64.33	29.3 ± 45.7	11/5/2007	13:50	0.50
75770	Y	29	33	34.2	22.5 ± 29.1	11/25/2007		0.50
75771	Y	9	16	87.66	42.2 ± 49.9	11/21/2007		0.48

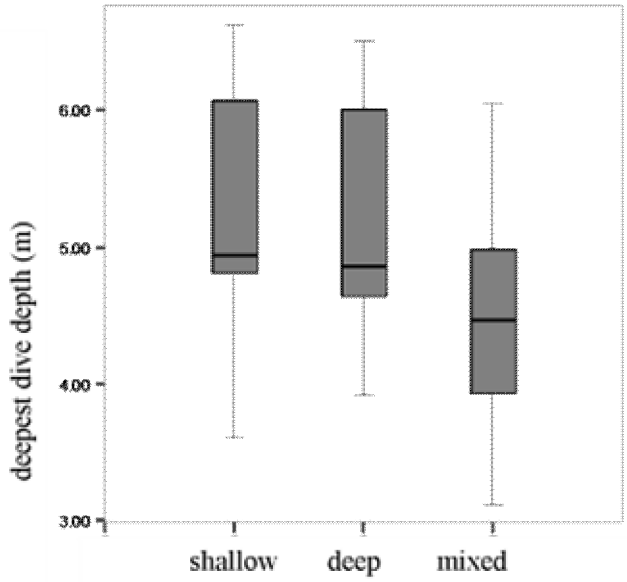

Fig. 16. Deepest dive depths recorded for each diving strategy identified.

The average foraging depths were compared among deep, shallow and mixed divers for ingestion events > 5 min and only through 15 December, 2007 when all three groups were still transmitting data. There was no significant difference ($p = 0.428$, Chi-squared = 1.698, df = 2) among the shallow (mean = 4.96 $\pm$ 0.72 m, N = 7), deep (mean = 5.14 $\pm$ 0.85 m, N = 9), and mixed divers (mean = 4.52 $\pm$ 1.06 m, N = 9) in average foraging depths. There was no correlation between the deepest depths recorded during a foraging dive and the duration of an ingestion event (Spearman correlation = 0.01, $p = 0.748$, N = 1098). Therefore, dive depths could not used to estimate ingestion event duration.

Similar to temporal observations of dive durations (Chapter III), shallow divers conducted 90.5% (N = 221) of their successful feeding dives during the night-time hours 1700 – 0500 local time (-12 UTC) from November – December, whereas deep divers conducted only 85.9 % (N = 213) of successful feeding dives during the night and evening hours. However, this is likely because deep divers dove more consistently throughout the day and night (Fig. 17).

Two shallow divers had foraging depth records that continued into January, therefore, several deep dives by shallow divers also were recorded during local daylight hours: 1000 – 1200 (-12 UTC). Despite the occurrence of daytime dives, only 16.5% (N = 42) of successful foraging events by shallow divers occurred during the daytime. Those January daytime dives by the two shallow divers were not associated with water ingestion events alone (mean = 19.41 $\pm$ 13.75 min), and indicated that at least some foraging behavior occurred during the daytime. The lack of data on the foraging depths and durations of any deep-diving individuals in January prevented comparisons between the shallow and deep diving strategies later in the migratory period.

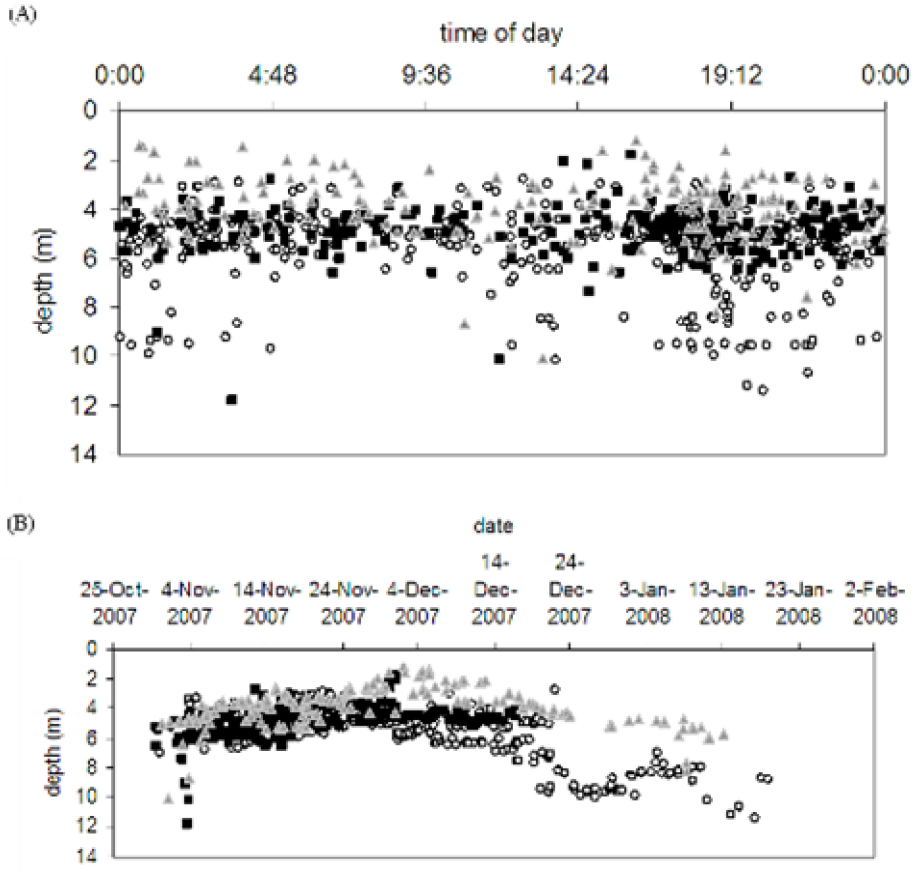

Fig. 17. Deepest depths recorded during an ingestion event for individuals using different dive strategies (open circles = shallow divers, black = deep divers, grey = mixed divers) for (A) time of day for all months combined, and (B) time since instrumentation.

Location of Ingestion Events

The locations of long ingestion events were determined for 21 animals that had 3 or more long (i.e., > 5 min) ingestion events. Pups encountered warm core eddies more commonly than cold-core eddies for all months (November – January). Although warm-

core eddies were encountered more commonly (2.03 $\pm$ 0.706 eddies month^{-1}) than cold-core eddies (1.42 + 0.507 eddies month^{-1}), this difference was not significant (Wilcoxin signed rank test Z = -1.71, p = 0.087). Ingestion events (N = 215) associated with warm core eddies made up 45% of the known locations of foraging behavior, associations with cold core eddies made up 16.3% of the foraging event locations, and the remaining 38.1% of foraging locations were not associated with any eddies. Most of these ingestion events were associated with the periphery of an eddy (Fig. 18), although some ingestion events did occur closer towards the center.

Discussion

This was the first study to use stomach temperature telemetry in free-ranging pups. The satellite-based technology proved that relatively complete foraging records can be obtained for up to 11.5 weeks, which exceeds the maximum retention time of 8 weeks recorded for harp seals (*Phoca groenlandica*) (Gales & Renouf 1993), and 5.7 weeks for grey seals (*Halichoerus grypus*) (Austin et al. 2006). However, a more realistic average of three-weeks is expected for most transmissions based on the median transmission end date for STTs in this study. In contrast, retention times of STT averaged only 16 days in free ranging adult grey seals (Austin et al. 2006), seven days in captive northern elephant seals (*Mirounga angustirostris*), and only 12 days for captive California sea lions (*Zalophus californianus*) (Kuhn & Costa 2006). The continuation of location and dive histogram data collection beyond the period of stomach temperature transmissions indicated that mortality was not a likely cause for the termination of most

stomach temperature transmissions in this study. This finding supports the use of stomach temperature telemetry in other young seals as a method to gather useful information on foraging behavior, with few adverse effects to young animals.

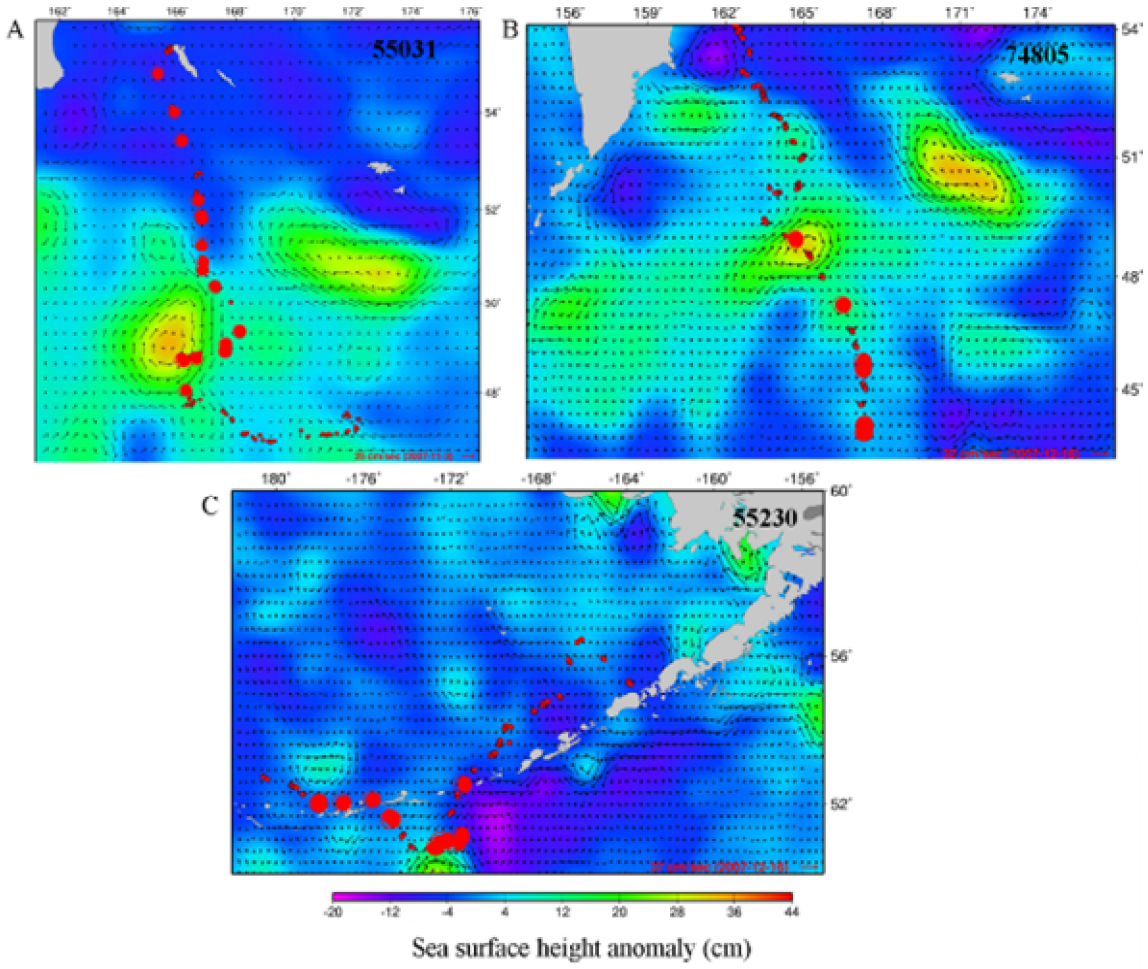

Fig. 18. Locations of long ingestion events (large circles) showing movement along (A) the periphery of warm-core eddies, (B) through the center of warm-core eddies and (C) along the edge of warm and cold-core eddies.

Some issues with using satellite transmission of stomach temperature data were problematic. The pre-programmed ingestion event start and end status messages were helpful in identifying the majority of ingestion events, but I still needed to visually inspect plots of stomach temperature profiles to accurately identify all ingestion events, and remove erroneously recorded ingestion events. Some incorrect triggers of high resolution recording were caused by a sudden peak in stomach temperature (above 38˚C) for one minute, followed by a return to normal body temperature the following minute. Peaks in stomach temperature for short periods of time may have been caused by problems with data recording, or alternatively as the result of corrupted status messages sent through Service Argos.

Another problem with using satellite telemetry to send large numbers of stomach temperature status messages was that not all status messages were retrieved each day. This may have occurred because the antenna on the SLTDR was not exposed long enough when the animal surfaced to transmit all data, or because satellite coverage was low whenever the animal surfaced. This could have resulted in the observed gaps in stomach temperature data, and caused the missing start and end messages for particular ingestion events, even though high resolution messages during that ingestion event were received.

Despite these problems, no other study has been able to identify when and where foraging behavior occurs in northern fur seal pups during their migration. Mariposa (sea water ingestion) was identified in all individuals, and occurred throughout the day. Successful foraging events resulting from prey capture were best determined by the

shape of the stomach temperature profile, and the time needed for recovery of normal body temperature (ingestion event duration).

Although successful studies in captive pinnipeds have estimated meal size by calculating the area above the curve in a stomach temperature profile (Gales & Renouf 1993, Hedd et al. 1996), the large number of variables related to the effects of meal size on stomach temperature, and the lack of studies calibrating meal size to change in stomach temperature using captive seal pups, has made a true quantitative measure of meal size unfeasible in this study.

The foraging behavior of northern fur seal pups early in the migratory period also suggested foraging behavior occurred at different depths than expected based solely on the shallow and deep diving strategy (Chapter III). In this study, shallow and deep diving pups did not differ in their foraging depths. However, shallow divers showed progressively deeper foraging dives over time. Moreover, the absence of deeper foraging dives in deep-diving pups may have been due to early termination of stomach temperature records for all deep divers. As expected, the shallow diving pups foraged mostly during the evening, night and morning hours, whereas deep-divers also exhibited long ingestion events during the day.

The occurrence of most long duration ingestion events during the night and evening hours in shallow diving pups supported the hypothesis that shallow-diving pups forage mainly on vertically migrating prey. However, the occurrence of several successful deep, daytime foraging dives was also recorded for two shallow diving individuals in January. This was contrary to the hypothesis that only deep divers forage

during the day. These two individuals did not travel more than 10 degrees east, but moved mostly south during their migration. This means that the local daytime hours used in the analysis (-12 UTC) corresponded to daylight hours experienced by these pups in their new locations, and thus, the daytime foraging recorded in these shallow diving pups was not due to changes in time zone later in their migration.

Interestingly, the deep daytime foraging dives (> 10 m) by the two shallow divers were recorded through stomach temperature telemetry, but not in their dive histograms (Chapter III). This may have resulted from missing or corrupted status messages in the satellite transmissions of dive histogram data. However, the relatively small number of deep daytime dives recorded in shallow divers and the lack of deep dives between 1200 – 1700 local time, still indicate that shallow divers prefer to make their deepest dives during the night and evening hours.

The deep diving pups foraged at depths similar to the depths recorded for juvenile walleye pollock, which do not vertically migrate. Pups did not appear to specialize their foraging by dive depths or time of day during the first two months of their migration. This indicates some overlap in their foraging strategies, and probably in their diets as well. There was no evidence to suggest that ingestion event durations differed between males and females, nor between shallow, deep or mixed divers, thus indicating no particularly advantageous strategy related to sex or foraging behavior.

Changes in the diving behavior of shallow and deep diving pups beyond the first two months of migration (Chapter III) suggest that differences in the foraging behavior might increase later in the migratory period. Unfortunately, this study was unable to

capture such behavioral indicators of maturation, and conclusions regarding differences in foraging behavior among pups with different dive strategies cannot be formulated at this time.

In comparison with the eastern Pacific region, the Kamchatka Strait, which many seal pups followed southwards, is known to have a high occurrence of eddies (Stabeno et al. 1994) which would provide a more productive region for Bering Island pups as compared to Pribilof Islands pups. Bering Island pups appeared to take advantage of this; in that most associations of ingestion events were located at the periphery of warm-core eddies. This association has been documented in adult females (Ream et al. 2005), although actual foraging behavior was not documented, but rather foraging was assumed from diving records and time spent in the area.

The periphery of warm-core eddies have been substantiated as relatively productive areas, where some upwelling occurs to counter the downwelling that occurs in the center of warm-core eddies (Olson & Backus 1985, Tranter 1985). Although cold-core eddies also are regions where ingestion events are likely (Ream et al. 2005), the relatively low encounter rates by seal pups with cold-core eddies in this study decreased the probability for their association with foraging in cold-core eddies as compared to warm-core eddies.

Conclusions

Early in the migration, there appears to be no difference in foraging success rates among shallow, deep or mixed diving pups, or between males and females. Shallow and mixed diving pups also forage successfully during the day later in the migratory period,

and pups may not feed exclusively on vertically migrating prey. There was no significant difference in the deepest foraging depths among shallow, deep and mixed divers, but the early end of transmissions of foraging data from deep divers prevented a comparison of foraging behavior among dive strategies later in the migratory period. The higher encounter rate with warm-core eddies may be a factor in the occurrence of most ingestion events being associated with warm-core, rather than cold-core eddies.

CHAPTER V

COMPARISON OF EPIPELAGIC AND BENTHIC FORAGING MOVEMENT PATTERNS IN NORTHERN FUR SEALS (*Callorhinus ursinus*) AND NORTHERN SEA OTTERS (*Enhydra lutris kenyoni*)

Introduction

In marine mammals, the need to return to the surface to breathe requires efficient search strategies so that individuals can locate and capture prey during a dive. For predominantly benthic foragers, such as northern sea otters (*Enhydra lutris kenyoni*), individuals do not have to search the water column for prey, and they can concentrate their search efforts only once they encounter the sea floor. Once a profitable patch is found, individuals may choose to stay in an area to enlarge existing pits (Kvitek et al. 1993), which is one way that sea otters can maintain their high success rates while foraging. Epipelagic foragers, however, have to search for prey that can be found at various depths, and therefore their search patterns may differ significantly.

Previous studies have attempted to qualify the efficiency of search strategies by describing animal search patterns using principles borrowed from particle movements in physics. For example, particle movements can be classified as clusters of many short steps (similar to the convoluted paths of foraging animals) interspersed between much longer step lengths that mimic the long-distance movements of animals traveling between patches. If the probability distribution of step lengths (l) follow a power law: $P(l) = l^{-\alpha}$, then the pattern can be described as a Levy walk (that uses a fixed time-step

component), or a Levy flight (that uses the number of steps of the different lengths) (Schlesinger et al. 1993). Levy walks have been successfully used to describe animal movement in a wide range of taxa (Viswanathan et al. 1996, Atkinson et al. 2002, Ramos-Fernandez et al. 2004, Boyer et al. 2006), and they are also thought to maximize search efficiencies in a heterogenous environment if α is close to 2.

However, one of the problems with using Levy walks to describe the efficiency of search strategies in marine mammals is that it often uses 2-dimensional step lengths obtained from tracking data that are obtained when the animal is at the surface. This fails to account for the additional distances traveled during 3-dimensional dives that are also part of the foraging search strategy. Interestingly, Sims et al. (2008) showed that the distribution of dive depths (i.e., using the vertical movements as step lengths instead of horizontal movements) in several marine vertebrates also resulted in Levy-like search patterns that maximized foraging efficiency in prey fields that mimicked natural prey distributions. Levy movement patterns used to describe animal behavior are widely accepted as an appropriate method to model the way marine vertebrates locate prey over large distances.

In addition to identifying efficiency of search strategies, it is also important to understand the relationship between individuals and their environment. For example, calculations of search efficiencies do not provide information about the size of areas searched while foraging because Levy walks describe scale-free animal movements. A lack of understanding of the distribution of prey in the environment, or the size of prey

patches, may also result in erroneous interpretations of the processes that generated the Levy walks in the first place (Benhamou 2007).

Estimating the spatial scales of actual foraging behavior from animal movements can be achieved by looking for area restricted searches (ARS). During ARS, animals are likely to stay within a patch longer, and have more convoluted pathways. Area restricted searches can be identified in first-passage time models that calculate the time needed to cross a circle of a given radius that is subsequently moved along the path (Fauchald & Tveraa 2003), or by measuring the tortuosity of segments along a path by calculating the fractal dimension (D) (Tremblay et al. 2007) along a moving window of the animal path. The fractal dimension ranges from 1 (a straight line) to 2 (for very convoluted paths that nearly cover a plane) (Nams 1996), therefore in segments where D is high, ARS is likely to occur. The advantage of using D to determine the scales of foraging behavior in satellite tracking studies is that it can identify how path tortuosity varies at different scales, whereas first-passage time models require more frequent time measurements than are available from satellite data.

While most studies focus on either the efficiencies of search strategies (Benhamou 2007, Sims et al. 2008), or the identification of the scale or location of foraging behavior (Benhamou 2004, Tremblay et al. 2007) from animal movements, few studies have looked at both. This study was conducted to look at the spatial scales covered and the foraging efficiencies in a benthic and epipelagic foraging marine mammal. A more detailed comparison of the foraging efficiencies and directions of

travel were conducted between northern fur seal (*Callorhinus ursinus*) adult females and pups to determine if pups had foraging search strategies similar to adults.

The objectives of this study were: 1) to compare the differences in path tortuosity, as measured by D, in benthic-foraging northern sea otters and the predominantly epipelagic-foraging northern fur seals, 2) estimate the scale of foraging behavior from movement tracks in sea otters and northern fur seals, 3) compare the large-scale movement patterns of northern fur seal adult females to pups to determine if adult females had more directional travel to preferred foraging areas, and 4) identify whether northern fur seal pups and adults used Levy-flight patterns to search for prey.

Methods

Study Sites and Animals

The study on sea otter movement patterns and foraging behavior took place in Simpson Bay, Prince William Sound, Alaska (*ca*. 60.4° N, 145.5° W) (Fig.19). Behavioral observations were conducted from May to August 2007, and observations were recorded using a focal follow protocol from a 6 m skiff. The skiff did not approach foraging otters closer than 100 m during a focal follow. Focal follows were terminated if an individual showed signs of disturbance (e.g., displayed short, frequent non-foraging dives, or rapid swimming away from the skiff) for at least five minutes during an observation. At the end of a focal follow, the otter was approached not closer than 30 m to visually identify its sex from the presence of a penile ridge in males, or teats in females.

Foraging dive locations were determined with a GPS of the skiff's location and by estimating the distance and compass bearing to an otter whenever a foraging dive was observed. Actual dive locations were overlaid on a map of bathymetry (Gilkinson 2004; Noll et al. 2009) in geographic information software (ArcView 9.2, ESRI, Redlands CA) to estimate dive depths. The error in the distances between the otters and the skiff was estimated using the same protocol with a buoy of known location.

The study on northern fur seal pups was conducted using satellite telemeters attached to animals from the northwest rookery of Bering Island, Russia. A total of 17 male and 18 female northern fur seal pups were tagged with Mk10-AL satellite linked time and depth recorders, and six lactating adult females were instrumented with SPOT-10 satellite telemeters (Wildlife Computers, Redmond, Washington). The satellite telemeters used Service Argos to receive data and estimate animal locations.

Individuals were captured with a hoop net, anesthetized, and the telemeters glued to the center of the mid-back of pups, and to the heads of adult females, with epoxy. The length, girth and weight of each individual were measured, and no pups < 14 kg were used in the study. A STAT filter (available from www.seaturtle.org) was applied to remove all consecutive locations > 1,000 km apart, locations < 1 h apart, locations < 25 degrees apart, and locations requiring travel speeds > 5 km h^{-1}.

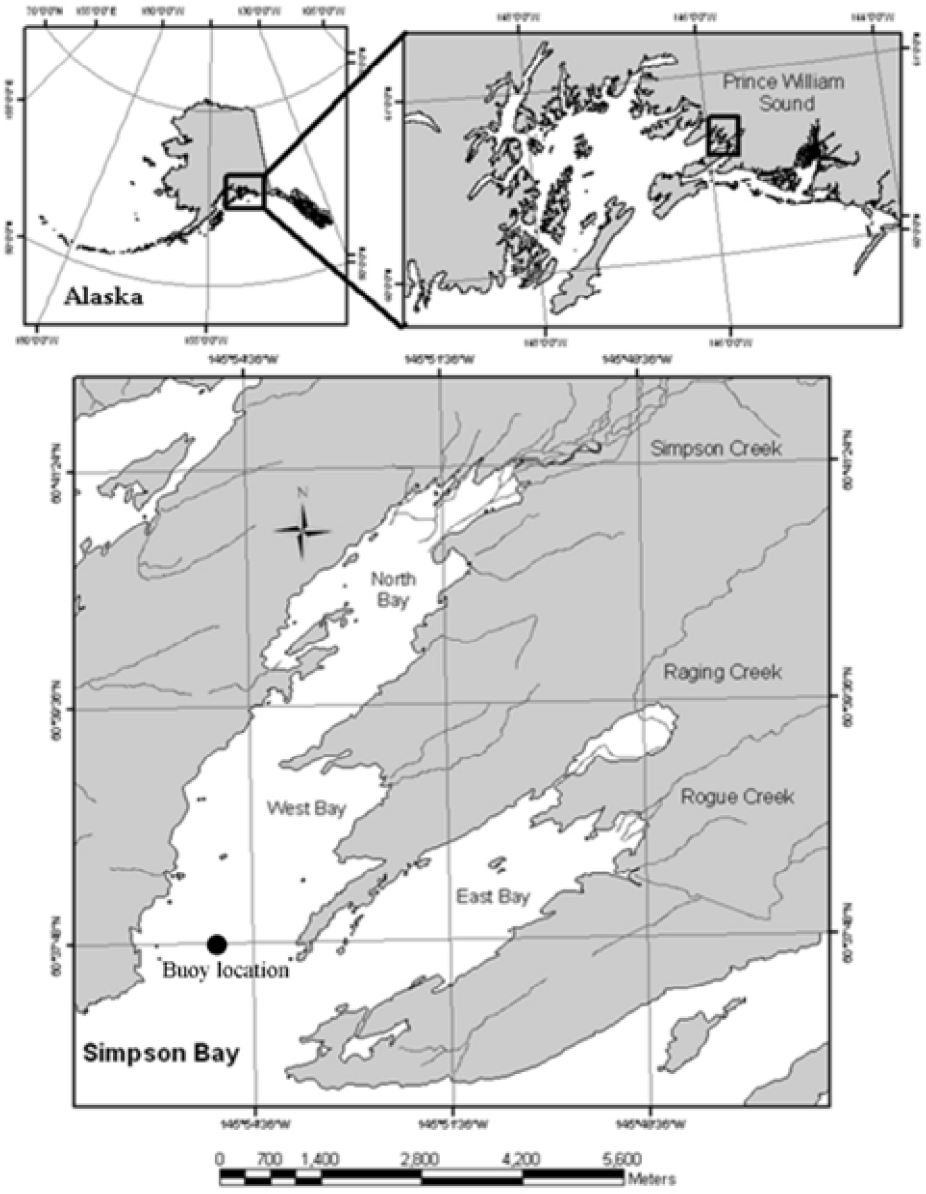

Fig. 19. Simpson Bay study area showing the three areas used for behavioral surveys.

Movement Pattern Analysis

Movement patterns can be described by path tortuosity, which in turn can be quantified by calculating the fractal dimension (D). This index ranges from 1 to 2, with

the most straight paths having a fractal dimension of 1, and more convoluted paths having values closer to 2. The simplest method of calculating D is using the dividers method, in which the dividers are straight lines that are walked along the entire path length to calculate the total path length. Different lengths of dividers are used to calculate the total path length. The traditional dividers method calculates the fractal dimension from the slope of a regression of the log step length (S), to the log total path length (L), using the equation: $L = S^{1-D}$. However, there are no error estimates for D using this method, and additional problems with truncations of calculations of path-length (Nams 2006a) make the traditional dividers method less desirable for estimating D.

Fractal dimension in this study were calculated using the VFractal estimator (Nams 1996) available from Nam's freeware Fractals.exe Ver 5.1.2600.2180 (http://nsac.ca/envsci/staff/vnams/Fractal.html). This method walks v-shaped dividers along the path length (Fig. 20) and allows estimates of error in the fractal dimension by bootstrapping. The correlation between cosines of the angles generated by the v-shaped dividers was used to indicate patch size. When the correlation between cosines of the angles is highly positive, animals are likely foraging at that scale (Nams 1996). The directedness of paths were estimated using the scaling test for oriented movement (Nams 2006b). This estimator works on the principle that non-directed movements sampled at large scales approximate correlated random walks, but directed paths sampled at larger scales would be much longer than a correlated random walk. The estimated parameter CRWDiff is positive if movements are oriented at large scales (Nams 2006b).

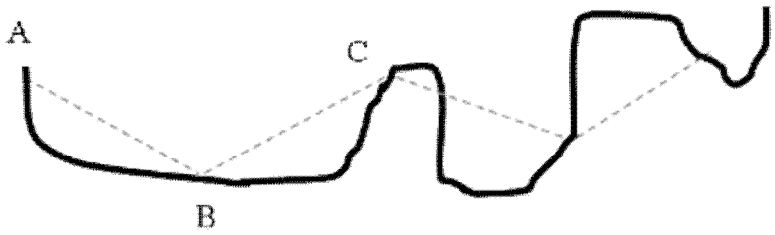

Fig. 20. Calculation of fractal dimension using V fractals in which the dividers walked along the path (solid line) are v-shaped (A-B-C) with varying scale lengths (line A-B).

Sea Otters

The VFractal dimension for sea otters were calculated using scale lengths ranging from 22 to 200 m, with 20 divisions within that range. Ten bootstrap replications along the path were used to generate a 95% confidence interval. The mean cosine of the turn angles was calculated and the significance of the similarity in successive turn angles was also recorded.

Fur Seals

The latitudes and longitudes of fur seal locations were first converted into Cartesian coordinates to more accurately measure the scales used to calculate the fractal dimensions. VFractal was calculated using scale lengths ranging from 0.5 km to half the observed path length (ranging from 33 km to 2425 km), with 50 divisions within that scale range for each animal. Ten bootstrap replications along the path were used to

generate a 95% confidence interval, and the mean cosine of the turn angles was calculated. The significance of the similarity in successive turn angles was also recorded.

A Levy-flight analysis was conducted to determine the effectiveness of search strategies in adult females and pups. This analysis could not be conducted on sea otters because their movements outside of a foraging bout were not recorded. The straight-line distances traveled from each filtered animal path were fit into 16 bins with upper limits of: 10, 20, 30, 40, 50, 60, 70, 80, 100, 110, 120, 130, 140, 150, 200 and 500 km. A log-log plot of the distribution of the straight line-segments was made to determine whether a power law relationship existed that would indicate Levy-like movements for each individual seal.

The initial choice of travel direction when animals left the rookery to begin their migration was identified using the windrose correlogram function from PASSAGE v.1 (Rosenberg 2001), which calculated the significance of preferred directions using the angles and distances between points. The significance between sectors in the correlogram was calculated using Moran's I test-statistic with simulations within sectors.

The correlogram is symmetrical, and therefore interpretation was emphasized using only the bottom half of the correlogram (Rosenberg 2001). Although the point locations of animals have a distinct directional aspect (i.e., there is a starting point, an ending point, and ordered points in between), the correlogram calculates reciprocal angles between points, and does not distinguish between starting point and ending point locations. However, because all individuals displayed mostly southerly movement

patterns, the windrose correlogram was only used to distinguish differences for adult females and pups in the east-west direction as they left the rookery.

Results

Northern Sea Otters

A total of 4,646 min were spent observing 1,354 foraging dives in 119 bouts. Foraging bouts lasted between 7 and 101 min with an average duration of 39.8 $\pm$ 20.6 min. The average water depth of foraging dives was 27.13 $\pm$ 19.86 m. The measured average error (using the buoy calibration) in the estimated distance from the skiff to an otter was 30 to 80 m, although greater accuracy was achieved at distances of $\leq$ 50 m.

Only paths that were greater than 2 km were used in this analysis which resulted in 29 useful foraging bouts. The average path length was 2.84 km, and the maximum was 6.8 km (Fig. 21). The mean of the maximum VFractal observed was 1.45 $\pm$ 0.35 at scales of 162.85 $\pm$ 60.1 m. The scale at which VFractal started increasing was 99.94 m, and this was similar to the value (98.04 m) where a peak correlation in cosine angles occurred, indicating that otters were foraging in patches at this scale. The mean correlation between sequential cosine angles was 0.044 $\pm$ 0.113, but the correlation was not significant.

Only 14 foraging bouts had positive CRWDiff values which showed movements that were more directed than a correlated random walk. The remaining 15 foraging bouts had CRWDiff values that remained negative at all scales. The mean scale in which

movements appeared to be more directed was 138 m ± 92 m with a range between 10 and 310 m.

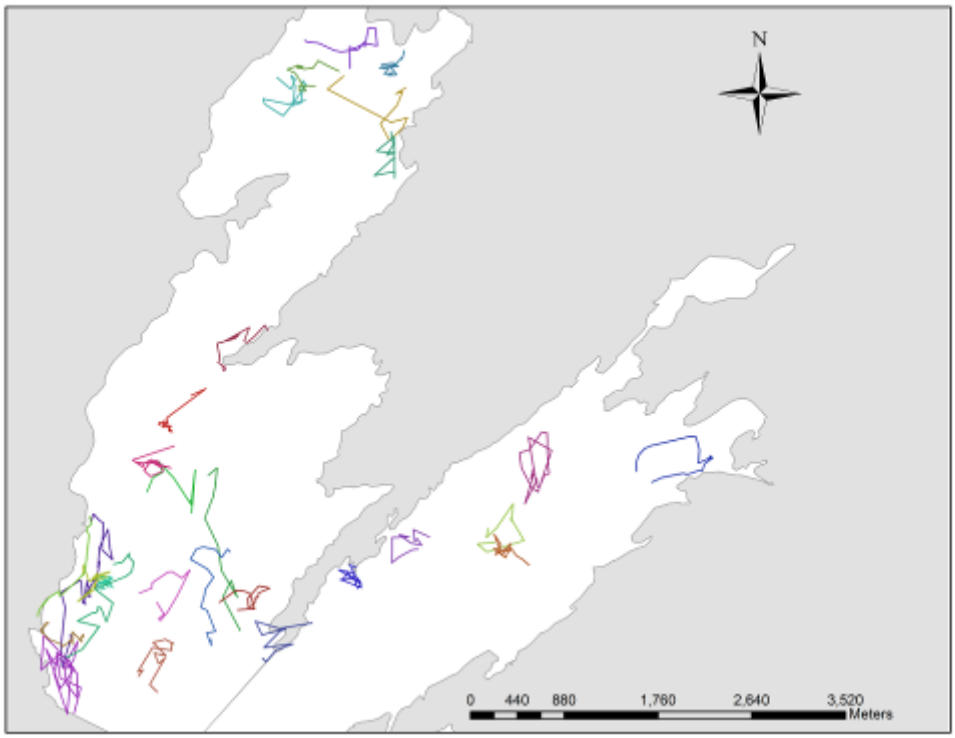

Fig. 21. Movement patterns of 29 individual sea otters in Simpson Bay.

Northern Fur Seals

A total of 32 pups and 6 adult females had path lengths greater than 100 km, and were used in the movement pattern and Levy flight analysis. Pup track lengths ranged from 572 to 4,850 km with a mean path length of 2,633.5 ± 1,087.2 km. Adult female path lengths ranged from 470 to 5,280 km with a mean path length of 2,718 ± 1,732.6

km (Fig. 22). The shortest path lengths were observed in individuals with the shortest satellite tag life.

For pups, the mean maximum VFractal was 1.21 $\pm$ 0.15 and occurred at a mean scale of 122.4 $\pm$ 80.6 km. The scale at which VFractal started increasing was 0.98 $\pm$ 1.36 km, and was within the range of the scales observed for the first peak in the correlation between cosines of angles (0.7 to 6.8 km). Additional peaks in correlation between cosine angles occurred at different scales and varied among individuals, but these peaks generally occurred anywhere between 15 and 150 km.

The CRWDiff was positive at scales > 1 km and remained positive at all scales for six pups. However, six pups showed a negative CRWDiff at intermediate scales, ranging from 9 to 50 km, indicating more directed movements at small scales and more random movements at intermediate scales. An additional 17 pups had negative CRWDiff values only at their largest scales, ranging from 16 to 270 km (Table 11), indicating very directed movements. The mean cosine angles for pups was 0.27 $\pm$ 0.09, and this correlation was significant for 19 out of 33 pups.

For adult females, the mean maximum VFractal was 1.25 $\pm$ 0.16 which occurred at a mean scale of 116.51 $\pm$ 83.86 km. The scale in which VFractal started to increase was 9.08 $\pm$ 10.87 km, and this was also within the range of the first peak in correlation between cosine angles (7.4 – 14.5 km). Additional peaks in the correlation between cosine angles occurred at scales of 24 to 74 km, and > 187 km, indicating patches at these scales as well.

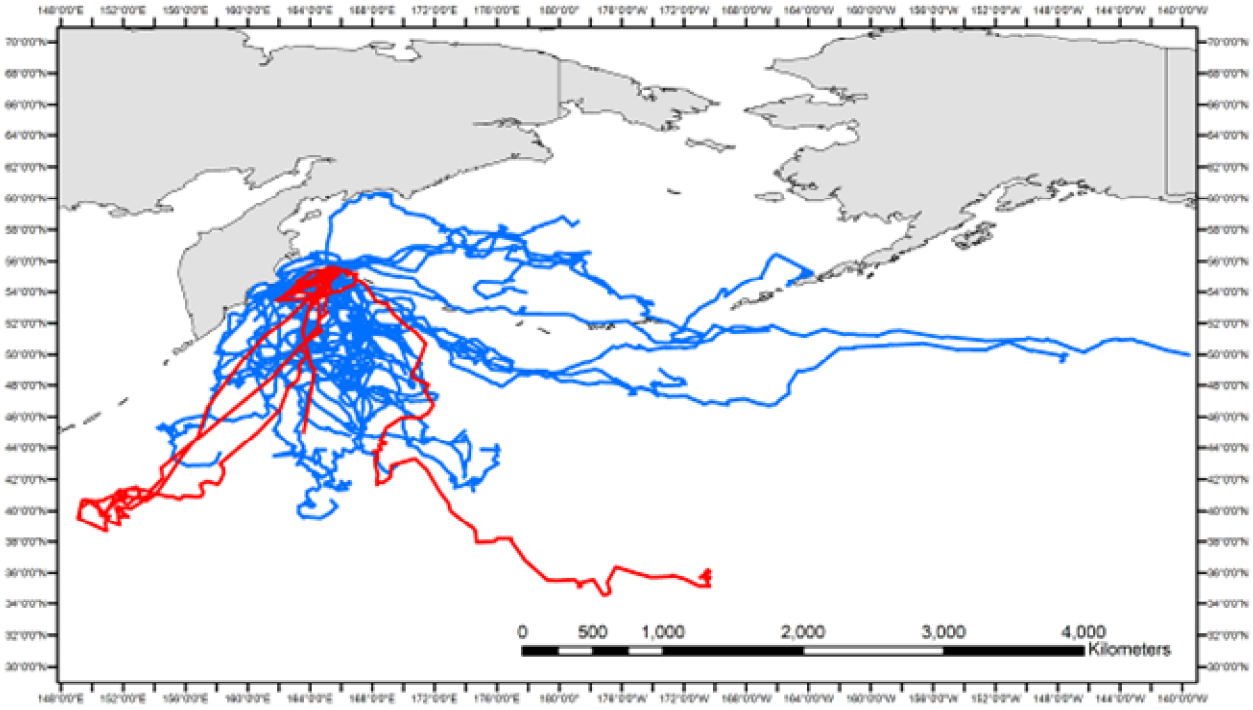

Fig. 22. Tracks of adult females (red) and pups (blue) used in movement pattern analysis.

The CRWDiff was always positive for scales > 1 km for two females, and was positive for scales > 5 km for one female, indicating very directed movements. Two adult females showed negative CRWDiff only at very large scales (292 and 309 km, respectively) indicating mostly directed movements as well. Only one adult female showed a negative CRWDiff at intermediate scales between 17.7 and 31.2 km, indicating more convoluted movements at this intermediate scale (Table 12). The mean cosine angles for adult females was 0.346 $\pm$ 0.121, but the correlation was not significant for 5 of 6 adult females.

The Levy flight analysis for individual pups showed a mean α value of 2.47 $\pm$ 0.46 which is close to the optimal value of $\alpha = 2$ for Levy walks. In adult females, the mean value of α was 2.62 $\pm$ 1.2. A Mann-Whitney U test, which was used to compare the non-normally distributed α values, showed no significant difference between adult females and pups (Mann-Whitney U = 73, p = 0.357, $N_{pups} = 32$, $N_{adults} = 6$).

Pup locations were positively autocorrelated at short distances in all directions (Fig. 23), indicated by the full segments in the inner-annulus. Although this correlation was significant, the correlation was relatively weak. The correlation in all directions indicated little preference for a particular direction at close distances (< 1000 km). At larger distances (> 1000 km) between point locations (segments in the outer annulus), significant positive autocorrelation was detected in the south-east direction for pups, and significant negative autocorrelation was detected in the north-south direction, indicating a preference for pups to travel in the south-east direction.

Mature females showed significant positive autocorrelation in the south-west direction over close distances (< 1000 km) (Fig. 24) between points. Over large distances, positive autocorrelation in the north-south direction was detected in mature females, but this was not significant (P > 0.05). However, at larger distances traveled there was significant negative autocorrelation in the east-west direction for mature females, indicating a directional preference to travel southward.

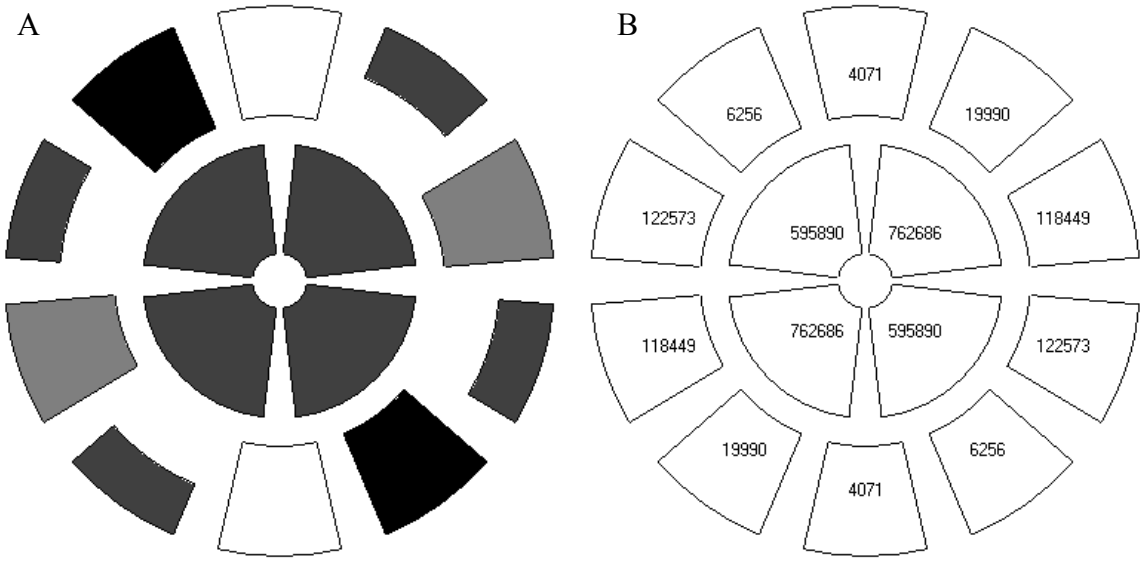

Fig. 23. Windrose correlogram of pup locations. Full segments (A) indicate significant angular correlation (Moran's I) and half segments are not significant. Dark colors show positive correlation, and light colors show negative correlation in a given segment. (B) number of pairs of points in each segment.

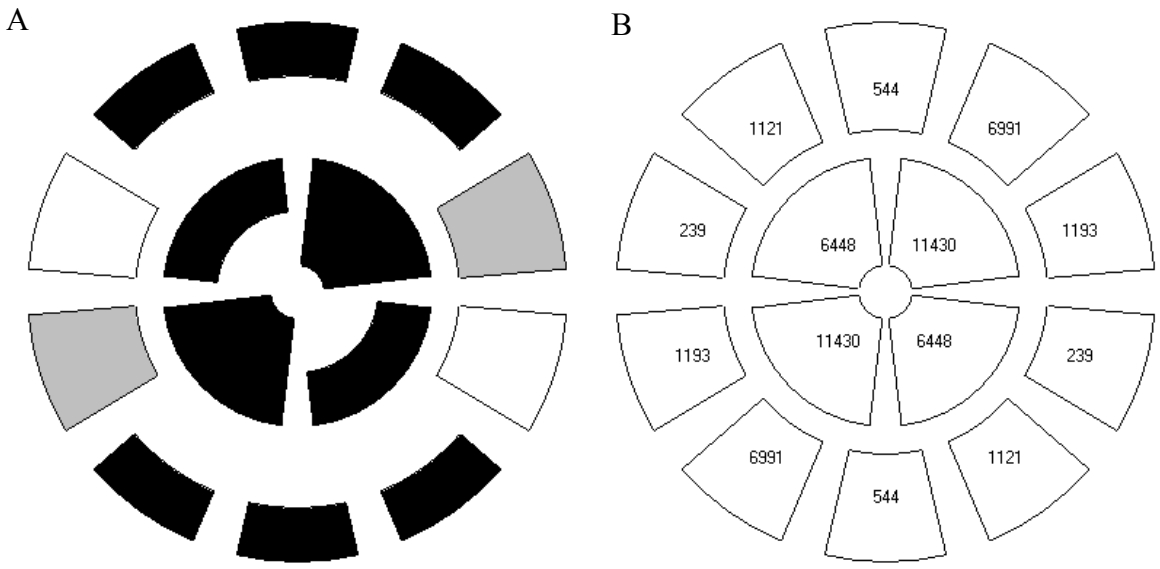

Fig. 24. Windrose correlogram of adult female locations. Full segments (A) indicate significant angular correlation (Moran's I) and half segments are not significant. Dark colors show positive correlation, and light colors show negative correlation in a given asymmetrical segment. (B) number of pairs of points in each segment.

Table 11. Individual movement pattern parameters for northern fur seal pups. *denotes significance for correlation between cosines of angles.

ID	Path Length (km)	Mean Cosine	MaxVFractal	Scale of Max Vfractal (km)	Scale for 1st peak in Cosine correlation (km)	Scale for 2nd peak in Cosine correlation (km)	Scale for 3rd peak in Cosine correlation (km)	CRWDiff Positive scale (km)	Levy α
55031	3741.7	0.284	1.42	224	0.7	2.8-4.4	11.5 - 15.1	1- 16.7	1.729
55230	4527.2	0.206*	1.09	315.1	1.1-3	15.3-129.8		>1	2.015
58079	2839.868	0.221	1.36	121.3	0.8- 2.4	3.7-7.2	19.3 - 43	1 - 28.1	2.194
58080	2402.9	0.234*	1.28	135.8	2.1-5.4	13.9-21.4	28 - 54.5	1 - 32	2.047
58083	1739.4	0.315	1.06	105.6	0.9-2.9	18.9-54.5	92.2	1 - 80.6	2.113
58084	733.413	0.128	1.22	51.07	0.7 - 2.6	11.8	20.8 - 24.5	1 - 3.39	3.447
58085	4850.2	0.411*	1.04	103.2	1.2 -5.3	12	52 - 149	1 - 270.3	2.090
58086	571.8	0.558	1.03	50.67	1.17 - 3.57	31	56	1 - 9.09	3.974
58087	3303.8	0.106*	1.155	45.2	1.1 - 4.5	9-33.2		1 - 114.7	2.405
58090	3960.99	0.184*	1.28	104.5	6.8	204.6		>1	2.466
58091	2751.85	0.314*	1.3	124.9	1 - 1.4	3.2	8.6 - 20.5	1 - 33.2, 40 - 151	2.263
58092	2446.5	0.3*	1.16	96.6	0.8 - 1.4	9.6 - 14.8	41.2 - 61	>1	2.231
58093	1206.9	0.178	1.09	61.1	0.9 - 2.1	3.5	6	1 - 72.5	2.735
58094	3017.8	0.245	1.29	173.3	0.9 - 3.6	6.2 - 8.2	13.7	1 - 20.7	2.376
58095	2899.7	0.273*	1.1	54.3	1.5 - 3.1	16.3 - 29.5	76.5	1 - 241.3	2.457
58096	1836.99	0.235*	1.26	93.8	1.4 - 4.7	24.8 - 55	106.2	1 - 34.4	2.381
58097	2695.31	0.231*	1.11	40	6.9 - 24.7	94.6 - 149.7		>1	2.400
58098	2532.9	0.07*	1.23	61.7	1.4 - 4.5	12.8 - 18.9	31.8 - 61.5	1 - 62.6	2.432
58099	3459.9	0.25	1.26	143.4	3.9	23 - 46	128.7 - 171	>1	1.857
58100	2081.56	0.345*	1.07	178.7	1.1 - 2.1	5.9	66.1 - 131	1 - 44.8	2.325
58101	919.8	0.355*	1.06	58.7	1.03- 2.9	8.18	26.6 - 38.8	114.2	3.416
74801	2948.3	0.286	1.37	119.6	0.7-1.9	9.4 - 15.2	159	1 - 160	2.359
74802	2523.5	0.271*	1.42	124.4	0.8 - 3.2	76.8	138.5	1 - 11.4	2.578
74803	1445.6	0.391	1.086	99.2	2.8 - 3.1	7.3 - 8.9	40	1 - 22.2	2.848
74804	2447.8	0.303	1.12	33	1 - 5.4	19.4 - 32.3	44.7 - 88.6	1 - 139.7	2.513

Table 11. continued

ID	Path Length (km)	Mean Cosine	MaxVFractal	Scale of Max Vfractal (km)	Scale for 1st peak in Cosine correlation (km)	Scale for 2nd peak in Cosine correlation (km)	Scale for 3rd peak in Cosine correlation (km)	CRWDiff Positive scale (km)	Levy α
74805	2089.7	0.185	1.12	165.3	0.7- 2.3	5.4	25.5	>1	2.388
75758	2803.2	0.292	1.16	84.6	0.9 - 3	12.5 - 20	74.6 - 93	>1	2.179
75759	2728.8	0.312*	1.4	98.3	1.4 - 1.6	9.1 - 23.1	46.2 - 53	1 - 18.4	2.708
75768	2939.1	0.342*	1.45	147	3	13	31.6- 54	1 - 20	2.405
75769	4250.5	0.288*	1.58	225.9	5.7 - 6.5	19.7 - 23	139.7 - 183	1 -29.2	2.273
75770	1291.7	0.247*	1.05	70.9	0.9 - 7.5	40.7	-	>1	2.995
75771	4268.8	0.311*	1.026	404.7	0.8 - 1.8	2.5 - 4.2	69.8 - 98	1 - 162.1	2.367

Table 12. Individual movement pattern parameters for adult female northern fur seals. *denotes significance for correlation between cosines of angles.

ID	Path Length (km)	Mean Cosine	MaxVFractal	Scale of Max Vfractal (km)	Scale for 1st peak in Cosine correlation (km)	Scale for 2nd peak in Cosine correlation (km)	Scale for 3rd peak in Cosine correlation (km)	CRWDiff Positive scale (km)	Levy α
44759	2095.3	0.527	1.07	46	46.2	74.2	-	>1	1.971
57540	1417.1	0.197	1.23	89.7	7.37	-	-	1 - 17.7	4.307
57541	470.2	0.258	1.55	11.98	9.7	-	-	5.06	4.02
57542	3613.3	0.365	1.2	159.6	10.8	> 64.8	-	<210.4	2.165
57554	5279.6	0.433*	1.18	241.1	7.7 - 9.1	24 - 40.3	246.4	<309	1.81
57555	3434.5	0.298	1.29	150.7	12.2 - 14.5	39 - 66.5	> 187	>2.7	1.485

Discussion

For both sea otters and northern fur seals, movement pattern analyses provided an estimate of patch size and the scales of foraging behavior. For sea otters, the Vfractals and correlations of cosines provided evidence for foraging in patches approximately 100 m apart. Benthic foraging at this scale supports the idea that sea otters stay within a chosen prey patch to enlarge existing pits, or to dig in nearby areas. Since clams are the main dietary item in soft sediment areas (Calkins 1978, Kvitek et al. 1992, Doroff and Degange 1994) such as Simpson Bay, staying in a small area to forage would be an efficient foraging strategy because individuals can use energy to excavate burrowing clams, instead of expending energy traveling between patches.

Northern fur seal pups and adult females exhibited foraging behavior occurred at more hierarchical-based scales. Such behavior would be expected for animals foraging over large areas with very patchy distributions of prey. Interestingly, in epipelagic foraging fur seals the maximum Vfractals for both pups and adults were smaller than in sea otters. This could indicate that sea otters were conducting area restricted searches with more convoluted search paths compared to fur seals.

However, an intraspecific comparison of differences in benthic and epipelagic search strategies in northern fur seals showed that the opposite was true with regards to path straightness. Using high resolution GPS, Kuhn et al. (2010) found that benthic foraging females had straighter and shorter search paths than epipelagic foraging females. It is possible that the straighter paths observed in the epipelagic foraging fur seals in this study were caused by the poor resolution of fur seal locations.

For pups, the first observed scale of foraging search behavior was observed at approximately 1 km with other peaks in foraging search patterns occurring between 15 and 150 km. Evidence supporting foraging behavior at scales of 1 km can be observed from the approximate travel speeds and durations of foraging bouts. For pups, the average travel speeds are 2.5 km h^{-1}, and the average foraging ingestion event was *ca.* 18 min (Chapter IV). Assuming that animals spend at least 5 min searching for prey before an ingestion event, foraging bouts would last at least 23 min. Based on the average travel speed and duration of a foraging bout, the estimated distances traveled during a foraging bout would be approximately 0.96 km, which is very close to the scale observed for the first peak in correlation in cosine angles.

The larger scales for foraging behavior in pups are likely patterns observed outside of a single foraging bout. Based on the frequency of successful foraging bouts (Chapter IV), it appears that individuals were not likely to forage successfully on consecutive days, and these larger scales of foraging behavior may result from the search strategies of multiple foraging bouts over a period of several days.

The adult female fur seals exhibited foraging behavior at several different scales as well. Compared to pups, the first scale of foraging behavior observed from increasing VFractal, and the correlation in cosine angles was much larger (*ca.* 10 km). Additional peaks were observed at scales of 24 to 74 km, and > 187 km. This was within the expected range for distances traveled within area restricted searches of *ca.* 37 km (Kuhn et al. 2010). Ream et al. (2005) estimated that the average swim speed of an adult in transit was approximately 2.1 km h^{-1}, and it is likely that the females in this study were

still in transit to preferred winter foraging grounds (Gentry 1998). However, even with an average foraging bout lasting two hours in adult females (Gentry & Kooyman 1986), the average travel speed would only allow the estimated distance traveled while foraging to be approximately 4.2 km, which is half of that estimated in this study.

One possible explanation for the discrepancies in foraging scales would be if two foraging bouts occurred that were only separated by short breaks in time and location. The movement pattern analysis would be unable to distinguish between the convoluted movement patterns of two consecutive foraging bouts, and therefore, the estimates of the foraging scale from the movement patterns would be doubled. The larger scales covered by adult females during a foraging bout could also be a result of their better diving and search skills as compared to pups. The greater energy requirements of adults would also be consistent with needing longer foraging bouts and greater search areas to capture more prey than a pup would require.

The directedness of movements of travel for both pups and adult females was evident from the CRWDiff parameter; at scales > 1 km, movements of most pups and adult females were more directed than a correlated random walk. However, in the sea otter study that had more detailed movement patterns on a per-dive basis, the CRWDiff identified the scales at which movements were more convoluted. The CRWDiff metric is only useful if it can identify the scale at which the value changes from negative to positive, indicating the within-patch foraging scale of individuals. Unfortunately, the poor resolution of the ARGOS data for seal locations did not allow use of this metric.

In addition to the differences in scales of foraging behavior between adult females and pups, examination of the efficiencies of their foraging strategies allowed us to determine if pups improved their foraging strategies later in life. Based on the windrose correlogram, pups showed no particular directional preference when first leaving the rookery, whereas all adult females showed a preference to travel in the south-west direction. However, over shorter scales of consecutive animal locations, the mean cosine angles showed that pups were more likely than adult females to maintain their direction.

The strong directionality of adult females showed that once they left the rookery for their winter migration they were mostly in transit to a preferred foraging destination. In contrast, pups showed evidence of more convoluted pathways during the first 2 months of their migration, which indicates more frequent foraging bouts early in their migration.

Considering the strong directionality of adult females early in the migration, it is understandable that some adult females did not show optimal Levy-like movements. In general, pups and adult females did not differ in values of α, which indicated they had similar efficiencies for search strategies. However, poor fit to the power law distribution was observed for path lengths of two adult females that were tracked for less than 2 months. For movement patterns that did not appear to be Levy flights, individuals traveled mostly in short segments, with very few large-distance trips between patches. In those few instances, the relatively short tracking period may have prevented capture of

enough data to show the full range of movement patterns required to identify Levy flight movements.

This study showed some of the challenges with using low-resolution location data for animal movement patterns to identify foraging strategies. The estimates of fractal dimensions in fur seals should be treated cautiously, as the maximum values of D reported here were 19% greater than the expected value for foraging fur seals obtained using higher resolution data (Kuhn et al 2010). Despite the limitations of using ARGOS data in animal pattern analysis, there was enough information to identify the foraging scales and potentially determine if animals are conducting Levy-like search patterns.

Conclusions

The movement pattern analysis was able to determine the approximate scales of foraging by individuals that moved between patches. The maximum D calculated for benthic foraging sea otters was higher than for northern fur seals. The use of certain metrics such as the CRWDiff was only useful in the sea otter study, because higher resolution animal locations were available. An additional problem with using low resolution ARGOS locations in analyses of movement patterns is that path tortuosity may be underestimated. Early in the migration, adult female northern fur seals showed more directed movements after leaving the rookery, and covered larger areas while foraging than did pups. Levy flight patterns were observed in adults and pups, although shorter tracking periods in adults made it more difficult to fit Levy-like patterns in adult females compared to pups.

CHAPTER VI

HABITAT ASSOCIATIONS OF NORTHERN FUR SEAL (*Callorhinus ursinus*) PUPS FROM BERING ISLAND, RUSSIA

Introduction

The "lost years" used to describe the mysterious period in juvenile turtle biology (Carr 1952) can be aptly applied to juveniles of many marine mammals that migrate into the open ocean. Northern fur seal (*Callorhinus ursinus*) pup behavior during their first two years at sea has only recently been described, and even those studies accounted for only the first year of this phase in their lives (Lea et al. 2006, Baker 2007). Individuals may not return to shore for up to two years after first leaving their rookery as 4- or 5-month old pups, and we know little about the many risks these naïve pups face. We also know very little about what hydrographic features pups associate with, although previous studies have identified some features preferred by older (aged > 3 years) animals (Sterling & Ream 2004, Ream et al 2005, Sterling et al. 2009).

The relatively long, pelagic, migratory phase of pups and our limited understanding of the environmental conditions they encounter make it difficult to understand the impact of the environment on pup survival. Estimates of survival rates before individuals reach the age of one year, can be as low as 53% (Barlow & Boveng 1991), which is the lowest survival rate experienced during their lifespan (Lander 1979). Causes of mortality in migratory pups are difficult to determine because individuals spend most of their time far offshore, and few bodies are recovered for necropsies. In

contrast, the mortality rate of pups still nursing on shore is much more easily quantified, and the causes of mortality can be easily determined (Baker & Fowler 1992, Boltnev et al. 1998, Spraker & Lander 2010). Although deaths of nursing pups have been attributed to disease, trauma and nutritional stress (Gentry 1998, Banks et al. 2006, Spraker & Lander 2010), the overall mortality rate of nursing pups is not thought to contribute as significantly to the declining Pribilof Islands (PI) population as is the high mortality rate experienced by pups after they depart for sea (Lander 1979, Calambodkis 1985, Chapter II). It is therefore important to understand the behavior and habitat associations of migrating pups in order to assess those factors that influence survival.

Pup migratory behavior has been described in seals from San Miguel Island (SMI) and the PI, which are both in the eastern range of the north Pacific. The pups from the small SMI population showed distinctly different habitat preferences from PI pups. SMI pups mostly stayed close to the North American coast with few individuals venturing past the continental shelf; whereas PI pups spent most of their time in open ocean water in the north Pacific and Bering Sea (Lea et al. 2006). Such differences in habitat use may result in exposure to different risks, which subsequently could affect pup mortality rates.

However, the small population size, and more southern location of SMI pups may not provide useful information for understanding how pup behavior can affect pup survival in the PI population. A more useful comparison could be with pups from the Commander Islands (CI), whose rookeries are closer in latitude to the PI, and whose population is more similar in size. Pups from the CI and PI may encounter similar

environmental conditions, but if behavioral differences exist, pup survival rates from these two populations still may differ. This study was the first attempt to identify the early migratory behavior of northern fur seal pups from the western end of their range. I examined the habitat associations of pups from Bering Island (BI) to determine whether they showed the same habitat use described in adults and juveniles from the PI.

One of the known habitat associations of adult northern fur seals and other marine predators is an association with mesoscale eddy peripheries that have enhanced productivity (Bailleul et al. 2007, Bost et al. 2009). Eddy peripheries tend to be more productive than the interior regions of eddies because there is a convergence (or upwelling in the case of warm-core eddies) of nutrient rich water in the eddy peripheries that supports phytoplankton and fish assemblages. The interior region of cold core eddies tend to be more productive than interior regions of warm-core eddies because upwelling of nutrient-rich water occurs within the eddy. The foraging success of pups could be improved if individuals spent significantly more time in eddy peripheries taking advantage of these regional concentrations of food resources. Other environmental factors that can indicate prey rich areas include chlorophyll a (chl a) concentration. Although this is only one of many pigments in phytoplankton, high chl a concentrations indicate productive regions with abundant phytoplankton, which supports a rich assemblage of zooplankton and fish (Olson & Backhus 1985, Hyrenbach et al. 2006) that in turn attracts larger marine predators.

Chl a concentration is also characteristic of the transition zone chlorophyll front (TZCF) (*ca*. 30 - 35˚ N in winter), where warm surface water from the south is known to

contain fish aggregations (Polovina et al. 2001). Apex predators including albacore tuna (*Thunnus alalunga*) (Laurs & Lynn 1991) and loggerhead turtles (*Caretta caretta*) (Polovina et al. 2000) use the TZCF for foraging, and similar use by seal pups could also improve their foraging success.

The prey rich areas in the eddy peripheries and TZCF are found mostly far from shore, and thus pups need to travel large distances from shore into deeper water to reach these areas. Therefore, increasing water depth and distance from shore should also be positively correlated to pup locations, particularly as time increases since pups leave the rookery.

I tested the following hypotheses for habitat associations of northern fur seal pups from BI: 1) pups spend more time in eddy peripheries compared to time in either central regions of eddies, or areas outside eddies, 2) pup locations are positively correlated with locations that have higher chl a concentrations, higher water temperatures (related to the TZCF), greater water depth, and greater distance from shore.

Methods

Study Site and Animals

Actual animal locations were obtained by attaching Mk10-AL satellite tags (Wildlife Computers) to 17 male and 18 female northern fur seal pups from BI, Russia. Individuals were tagged between 30 - 31 October, 2007 and were expected to begin their winter migration within a few weeks of being tagged. Therefore, only individuals with satellite tracks showing more than 2 weeks of time spent at sea were used to model

habitat associations. All animal locations were obtained from Service ARGOS and filtered using STAT (Godley and Coyne 2005) to remove locations that: 1) were > 1,000 km between consecutive points, 2) required extended travel speeds exceeding 5 km h^{-1}, and 3) did not pass the angle filter for being < 25 degrees apart. All locations on land were also removed from the database of potential animal locations.

Simulating Animal Locations

To model habitat preference, the actual pup locations were compared to locations on simulated tracks that represented the null hypothesis that pups have no association with measured environmental variables. Because animal tracks are serially auto-correlated in both space and time, the simulated tracks could not be simply randomly generated points. The simulation and logistic modeling used in this study were adapted from a study by Cameron et al. (2007). Using the observed distribution of travel speeds and bearings for the pups in this study, simulated tracks were created that conserved the same time lags between pup locations. The location effects of shorter time lags on travel speeds were obvious in the original plot of time and speed (Fig 25). Over shorter time periods, there was a greater range and variance of travel speeds than over longer time periods. To stabilize the variance, travel speeds speed was first transformed using the formula:

$$S = D/T^{0.5} \qquad \text{(equation 1)}$$

where S is the transformed travel speed, D is the distance traveled in km, and T = time in hours. However, this overcorrected the variance, resulting in greater variances for longer

time-lags. I empirically determined that the best transformation of travel speed was achieved using the formula:

$$S = D/T^{0.85} \qquad \text{(equation 2)}$$

which resulted in more stable variance for travel speed across all time lags (Fig. 26).

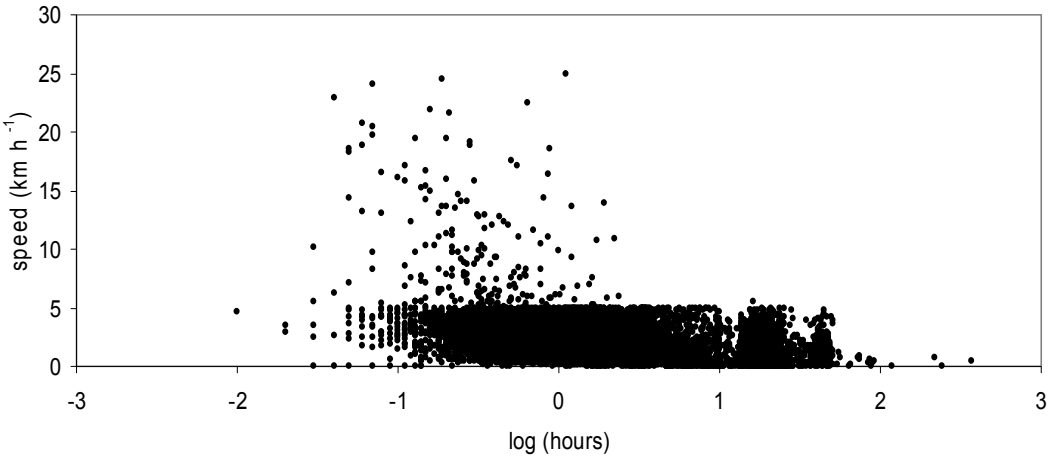

Fig. 25. Plot of untransformed travel speeds at different time lags.

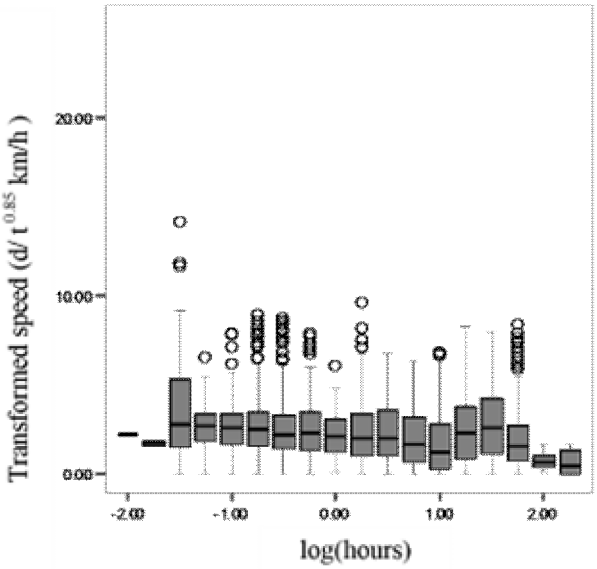

Fig. 26. Transformed travel speeds across time lags (log hours) showing stabilized variances in travel speeds.

The distribution of bearings were first compared between males and females using a one-way ANOVA. There was no significant difference between the mean bearings of males (N = 4,834, mean = 171.1, SD = 95.89) and females (N = 5,168, mean = 169.4, SD = 92.68) ($p = 0.356$, $F = 0.851$, $df = 1$); therefore, I pooled data for bearings and transitional matrixes across males and females. In both males and females, the trend for heading south to south-east, was indicated by higher frequencies of southern bearings (Fig. 27). However, to evaluate the effects of autocorrelation between bearings, I created a transition matrix of direction change between bearing groups.

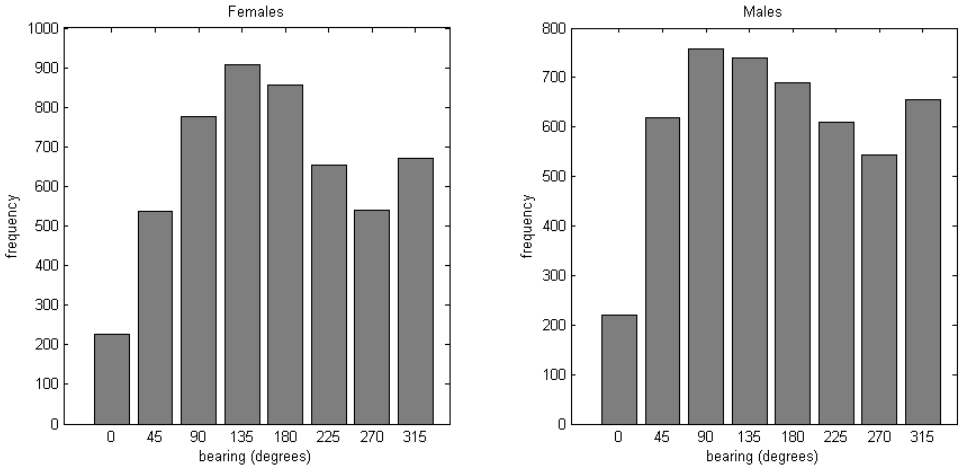

Fig. 27. Frequency of bearings chosen for males and females.

The transitional matrix described the probability of an individual's membership in a new bearing group, given its previous bearing group. Bearing groups were defined as the upper limit of the range in each category (Table 13; i.e., the first category included bearings > 0 and ≤ 45, the second category included bearings >45 and ≤ 90).

Table 13. Transition matrix of bearings grouped into 45 degree categories.

		Next bearing							
		45	90	135	180	225	270	315	360
Starting bearing	45	0.15	0.22	0.17	0.11	0.03	0.10	0.11	0.12
	90	0.11	0.20	0.18	0.14	0.12	0.04	0.10	0.10
	135	0.10	0.16	0.22	0.20	0.11	0.10	0.04	0.07
	180	0.06	0.13	0.18	0.24	0.17	0.11	0.09	0.02
	225	0.02	0.10	0.13	0.21	0.21	0.15	0.10	0.07
	270	0.09	0.05	0.13	0.16	0.15	0.20	0.15	0.09
	315	0.11	0.14	0.07	0.14	0.12	0.15	0.16	0.12
	360	0.17	0.18	0.13	0.05	0.09	0.10	0.13	0.15

The relationship between transformed speeds and bearings was modeled using the following equation:

$$TS^{0.2} = 0.0000017635*b^2 + 0.0006142*b + 1.0947 \qquad \text{(equation 3)}$$

where TS is the transformed speed (from equation 1), and b = bearing in degrees. The best fit model had an R^2 value of 0.453, and a residual variance of 0.547 (Fig. 28).

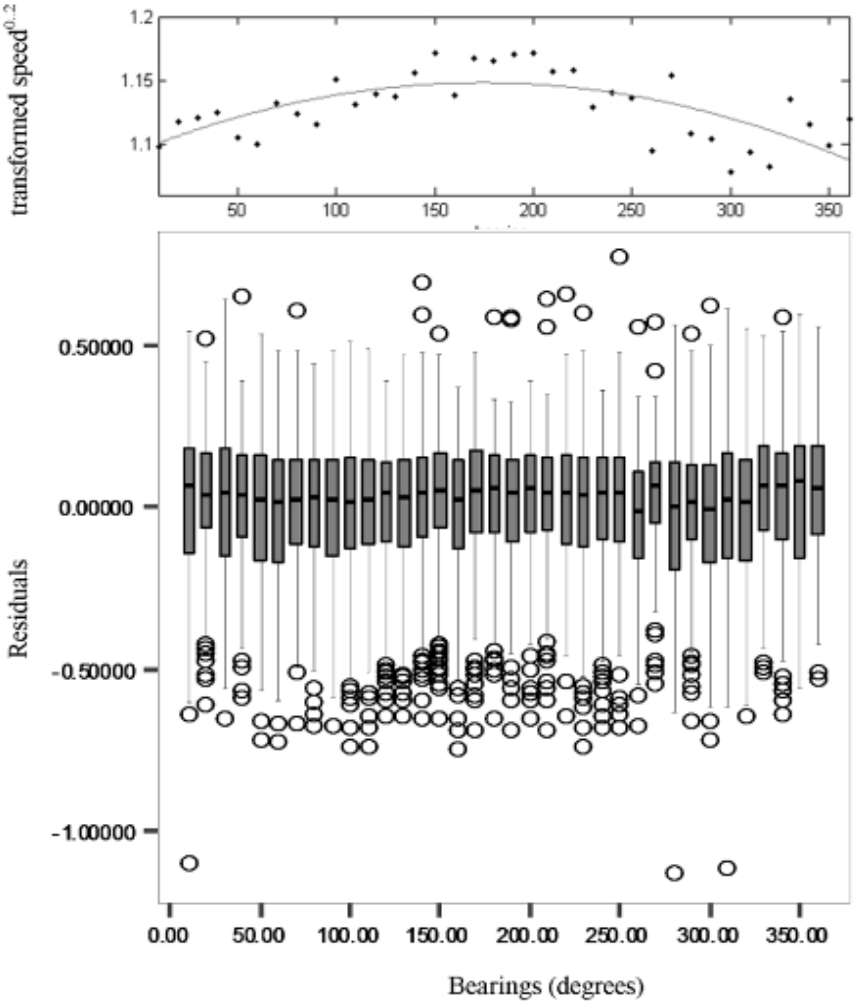

Fig. 28. Relationship between bearings and transformed speeds and associated residuals of speeds for bearings grouped into 10 degree classes.

The bearing transition matrix, and the relationship between travel speeds and bearings, were included in a MATLAB model that simulated new bearings and travel speeds using the same time lags as observed in each animal track. All individuals started with a bearing of 180 degrees from the rookery. The transition matrix was used to determine each successive bearing using a random uniform distribution of angles within each bearing class. The relationship between travel speeds and bearings was used to model the travel speed given the simulated bearing. Distance traveled between locations was calculated by back transforming travel speeds to km h^{-1} and using the known time lags between locations for each animal track. Ten simulated animal tracks were created for each tagged pup. Any simulated locations that were on land were removed, and the process of simulating bearings and travel speeds was repeated to find new simulated animal locations.

Environmental Variables

The environmental covariables were obtained from different sources to cover a region in the north Pacific and Bering Sea between 140^{o} E and 140^{o} W and 38^{o} to 61^{o} N. These variables were imported into ArcGIS 9.2 for further analysis. Inverse distance weighting was used to create a continuous surface from discrete data points for sea surface temperatures and chl a concentration. The sea surface temperature (˚C), and chl a concentration (mg m^{-3}) were determined on a monthly basis from MODIS-Aqua satellite data that were produced with the Giovanni online data system developed and maintained by the NASA GED DISC. Bathymetry data were obtained using ETOPO1 global relief (Amante & Eakins 2009).

The location of the centers and sizes of eddies present in the North Pacific were determined using a modified MATLAB program that used sea surface height anomalies and current velocities to detect mesoscale eddies (Balasubramanian et al. 2003). Mesoscale eddies were detected on a biweekly basis between November 2007 and March 2008. The altimeter products used for eddy detection were produced by Ssalto/Duacs distributed by Aviso, with support from Cnes (http://www.aviso.oceanobs.com/duacs/). Although the actual sizes of mesoscale eddies were detected in this program, the habitat association model considered animal locations to be in periphery of an eddy if it was greater than the mean radius (70 km radius) from the eddy's center.

The actual and simulated animal locations were imported into ArcGIS 9.2 where values for the associated environmental variables were obtained for each location. The distances from: the shore, the center of the closest eddy, and the peripheries of the closest eddy, were calculated using GIS algorithms.

Modeling Habitat Associations

The autocorrelation between animal locations was minimized by using each track as a sample instead of individual locations. For each of the ten pairs of actual and simulated tracks (with each track containing the same time lags between animal locations), a binary logistic regression model was run using SPSS 15.0. The dependent variable was a predictor of presence or absence (0 or 1) of a pup, and the hydrographic variables were the covariates. Each of the covariates had its own regression coefficient whose magnitude and direction (positive or negative) indicated the strength of the

habitat association (strong or weak). The magnitude of the correlation (positive or negative) for each hydrographic variable determined the likelihood of a pup being associated with that variable.

All continuous variables (depth, SST, chl a concentrations, distance from eddy centers, distances from shore) were first square root transformed to convert long tailed distributions to more symmetrical distributions. The presence of long tails in distributions would have affected the regression coefficients, which could result in a biased association with a habitat variable. The Monte Carlo approach (Manley 1997) was used to estimate the variance, mean, and standard errors of the logistic regression coefficients by running 10 independent fits of the model. The null hypothesis (regression coefficients equal to zero) was tested without the use of a likelihood-model based criteria (e.g., AIC). Instead, the best fit model was determined by the stepwise addition of environmental variables that had significant ($\alpha < 0.05$) regression coefficients using p-values that were generated from the Monte Carlo simulations of each logistic regression model. All variables having non-significant regression coefficients were excluded from the final model. This method produced a final model in which the regression coefficients indicated the magnitude and direction of pup associations for all significant habitat variables.

Associations with Eddy Peripheries

Potential preference for eddy peripheries was investigated using the actual eddy radii generated from the eddy detection program (Balasubramanian et al. 2003). The animal locations were compared to the biweekly detection data for eddies. The eddy

periphery was defined as the region within 10 km either inside or outside of the eddy boundary (i.e., eddy radius $\pm$ 10 km); the internal region of the eddy was from the center of the eddy to the inner edge of the eddy periphery. The number of actual animal locations observed in the periphery and internal regions of all eddies encountered were measured in ArcGIS to approximate time spent inside each region of the eddy.

The preference for cyclonic and anti-cyclonic eddies was investigated by counting the number of animal locations in biweekly detections for each eddy type. The time spent by animals in the different regions and different types of eddies were then compared using a Wilcoxin signed rank test, and a Mann Whitney U test (respectively) using SPSS 15.0.

Results

The simulated animal locations were generally clustered in the southern and western regions of the north Pacific (Fig. 29) where there was a lot of overlap with actual animal locations. All environmental variables showed good coverage over the north Pacific study region, except chl a concentrations, which had large regions with no data in November and December at latitudes 46˚N and higher.

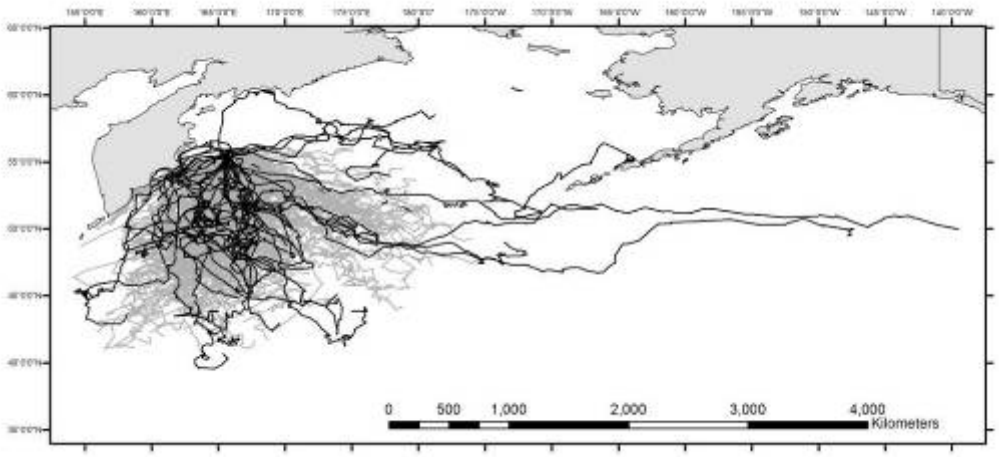

Fig. 29. Simulated animal tracks (grey) and actual animal tracks (black).

Of the 10 logistic regression models, 58.8% to 71.8% (mean = 0.64, SE = 0.01) correctly predicted animal location (Table 14). The final habitat selection model, which only included significant regression coefficients was:

0.857*chlorophyll + 0.742*distance from shore + 0.189*SST – 0.022*depth

The covariables distance from eddy center and eddy periphery, and the interaction term between chl a and eddy peripheries were not significant, and did not improve model fit. The order of importance for variables predicting animal location were: increasing chl a concentrations (Fig. 30), increasing distances from shore, increasing sea surface temperatures (Fig. 31), and decreasing water depth. The mean exp(β) value (Table 14) is a measure of response effect for each covariable. For example, for each unit of increase in chl a concentration, the model predicted that an

animal was 2.402 times as likely to be found in that area; assuming all other factors were kept constant.

Table 14. Regression coefficient results from the ten logistic regressions. (SST = sea surface temperature)

Covariable	Mean β	SE	Mean exp(β)	p
Chlorophyll a	0.857	0.06482	2.402	<0.001
SST	0.189	0.05184	1.1222	0.005
depth	-0.022	0.00119	0.9783	<0.001
distance from shore	0.742	0.06331	2.1372	<0.001
distance from eddy center	-0.018	0.12823	0.9511	0.891
eddy periphery	0.0487	0.11607	0.8364	0.685
periphery*Chlorophyll	-0.1513	0.15603	0.5562	0.358

The average number of all animal locations in the internal regions of eddies (mean = 16.3, SD = 17.9) was smaller than the number of locations in the periphery regions of eddies (mean = 18.1, SD = 88.5), and this difference was significant ($Z = 1.66$, $p = 0.008$). The high standard deviation for locations at the periphery was caused by one particular eddy located close to the rookery (Fig. 32). During the first two weeks of November when most pups were first leaving the rookery, they traveled along the periphery of that eddy, resulting in 846 locations counted in eddy alone. Excluding this eddy from the analysis resulted in fewer locations in the eddy periphery (mean = 8.87, SD = 11.5) than in the internal region of eddies (mean = 15.4, SD = 15.8), and this difference was significant ($Z = 8.27$, $p < 0.001$). There was no significant difference in

the number of locations found within a cyclonic or anti-cyclonic eddy ($Z = -0.047$, $p = 0.963$), indicating no preference for eddy type.

Discussion

The habitat association model for pup location predicted that pups were strongly associated with regions that: 1) had high chl a concentrations, 2) were far from shore, and 3) had higher SST, all of which were consistent with the two original hypotheses. Despite spotty coverage for chl a concentration during winter, pup locations were strongly correlated with regions with higher chl a concentrations. Generally, where large gaps in habitat data exist, the association with that habitat variable tends to become less significant, because fewer animal locations are associated with that variable. This was not the case for chl a, thus the strong correlation with chl a concentration implies a strong association for pups to regions with high productivity.

Within the TZCF, where there is a sharp gradient in chlorophyll concentrations, pups preferred areas with the highest chl a concentrations. In this study, the close association of pup locations with the highest chl a concentrations may indicate little time lag between the occurrence of enhanced primary productivity and the resulting increases in prey abundance (Tranter et al. 1985, Olson et al. 1994).

However this may not always be the case; instead, a delay between increased chl a concentration, and the associated increase in productivity that results in greater fish abundance is likely to occur (Baker et al. 2007). Such tight coupling between chl a and pup locations provides strong support for the advantages of increased productivity related to greater foraging success of pups.

The correlation between increased survival rates and foraging in the highly productive TZCF has not been explicitly documented in northern fur seals, but a positive relationship between first and second year pup survival and TZCF location was shown for Hawaiian monk seals (*Monachus shauinslandi*) (Baker et al. 2007).

The highest chl a concentrations were observed either very close to shore or far offshore in the TZCF. However, pups showed a preference for traveling far offshore, making their locations positively correlated with increasing distances from shore. One reason that pups do not utilize the productive regions close to shore may be that killer whales (*Orcinus orca*) frequently occur close to shore (Mamaev & Burkanov 2006, Burdin et al. 2007). The preference for traveling far offshore may be a predator avoidance tactic, in addition to finding productive off-shore regions.

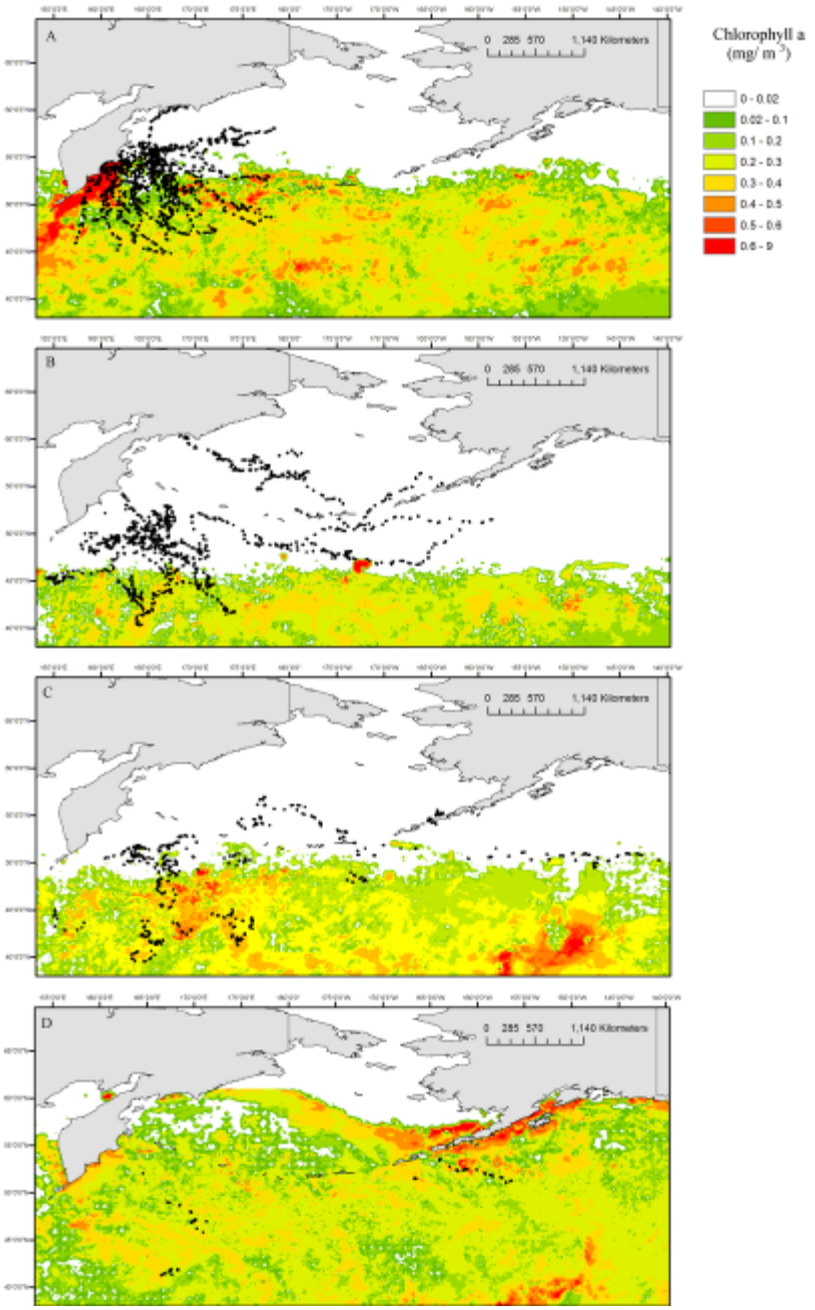

Fig 30. Actual animal locations at varying chl a concentrations in A) November, B) December, C) January, D) February.

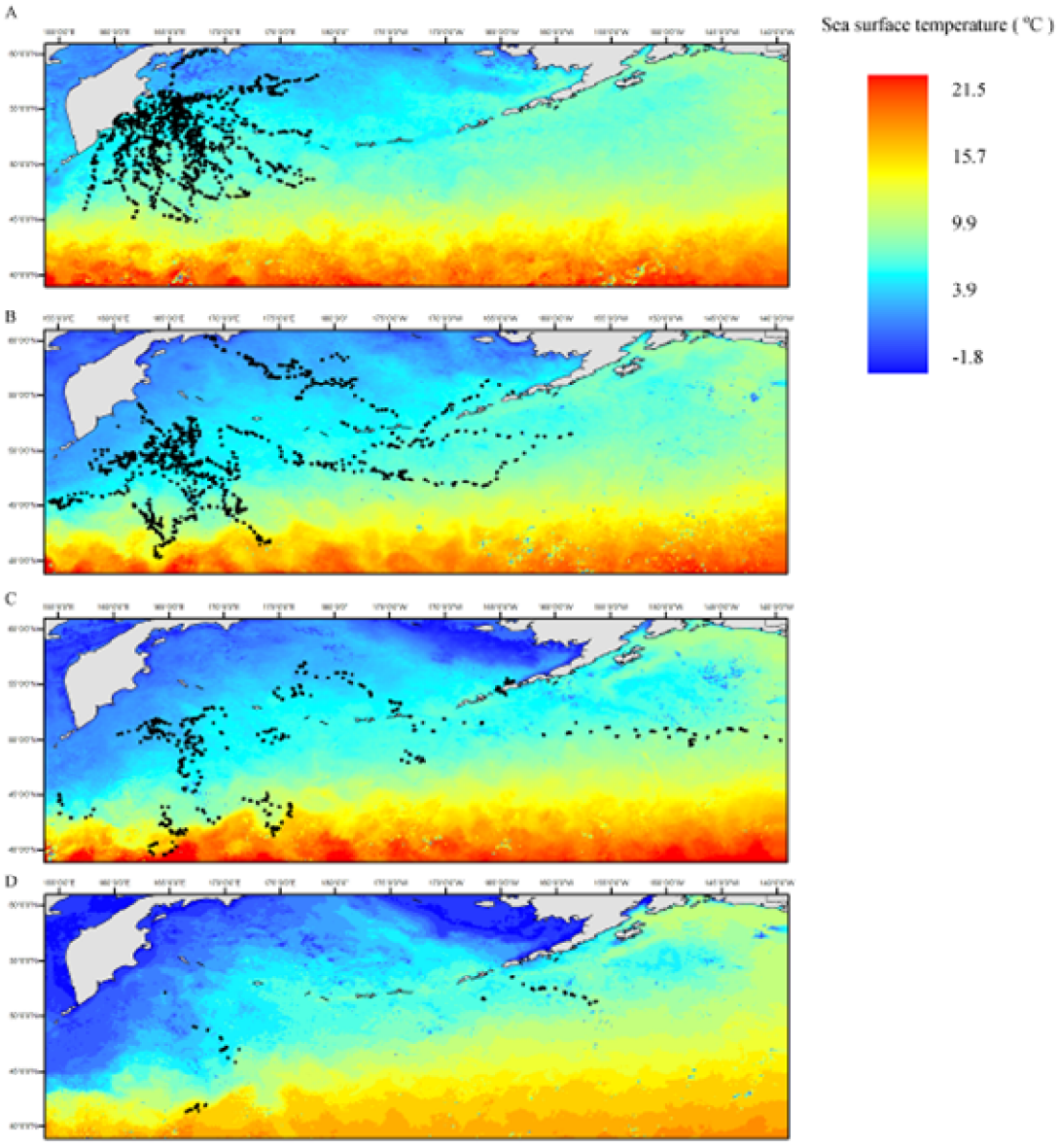

Fig 31. Actual animal locations at varying sea surface temperatures in A) November, B) December, C) January, D) February.

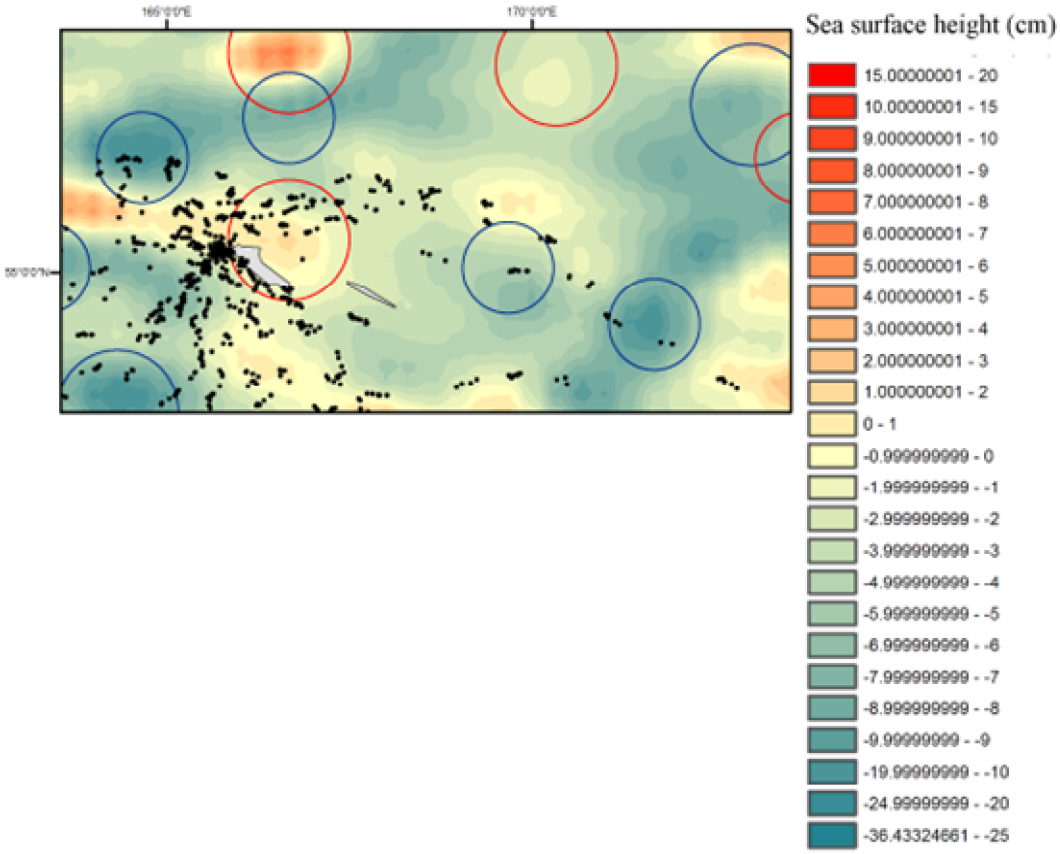

Fig 32. Animal locations with reference to sea surface height and eddy locations. Blue circles are cyclonic eddies, and red circles indicate anti-cyclonic eddies.

Although individuals did not remain over the continental shelf, they also were not attracted to the deepest water. Originally, I hypothesized that pups would be attracted to deeper water because of the general correlation between deep water and increasing distances from shore. However, northern fur seals do not dive deep enough to utilize benthic environments, and thus bathymetry may not be strongly related to preferred depths of foraging locations. Adult female northern fur seals also have been observed in water with bottom depths of less than 100 m (Ream et al. 2005), which is much

shallower than the average bottom depths in the North Pacific and Gulf of Alaska. Such observations are consistent with the hypothesis that individuals may be responding to prey depths rather than bathymetry.

The affinity that pups had for higher SST was not unusual and similar behavior has been identified in adult female northern fur seals foraging in the TZCF (Ream et al. 2005), immature Steller sea lions (*Eumetopias jubatus*) (Fadely et al. 2005), and some southern elephant seals (*Mirounga leonina*) diving in association with a polar front (Bailleul et al. 2007). The affinity for higher SST is not likely a result of a preference for warm-core eddies, because no such eddy association was found. Instead, the pup association with higher SST was most likely due to the large number of pups that encountered the TZCF early in their migration, and their tendency to forage in temperate, rather than subarctic environments during their first few months at sea. Interestingly the TZCF appeared to act as a barrier to pups, preventing them from traveling farther south to more tropical water. The SST and other physio-chemical cues may cause physiological constraints on both the pups and their prey (Neill et al. 1983), preventing southward movement beyond the TZCF.

The tendency for pups to travel south was captured well in the simulated pup locations that were created using the same pup directional preferences rules obtained from observed data. The Alaska Stream is the only major current moving in the east-west direction just south of Bering Island. This current moves westward, and would move pups towards the Kamchatka peninsula, which then discourages pups from moving

too far eastward. Upon encountering the Kamchatka landmass, pups would also be more likely to travel southwards.

Another possible reason that pups may prefer higher SST while in transit to richer foraging grounds is that behavioral thermoregulation is important for young pups, and seeking patches of warmer water may be advantageous. The thermoregulatory capabilities of northern fur seal pups in water are poor before they molt, thus limiting the time pups spend in the water while nursing (Baker & Donohue 2000). However, thermoregulation may remain difficult for pups that leave rookeries with poor insulation. The thermal neutral zone for northern fur seals pups is at least 16˚C, and below this lower critical temperature, their resting metabolic rates increases with decreasing water temperature (Liwanag 2010). Although the SST appears relatively homogenous within bands of latitude, individuals may track patches of warmer water as they are encountered.

The most surprising results from the habitat preference model were that pups did not prefer an eddy type (cyclonic or anticyclonic) or an eddy region (peripheries vs central), despite such preferences by adult females and older juveniles (Ream et al. 2005, Sterling et al. 2009). Two possible reasons for this lack of affinity to eddies include: 1) the Monte-Carlo logistic modeling method itself, 2) pups have not yet learned to detect the advantage of staying in more productive eddies.

It is unlikely that the Monte-Carlo logistic model itself influenced the results, even though problems with logistic models exist (Pearce & Ferrier 2000). The use of pseudo-absence data from simulating animal locations has been criticized for generating

incorrect models because they may not accurately determine suitable habitat in a region (Phillips et al. 2009). However, in the case of determining eddy affinity, a random pattern was generated from the simulated tracks, and it was not different from the actual animal tracks. The actual animal tracks were likely to appear random because individuals frequently traveled through eddies, and did not spend more time along the outside of eddies. Increased diving behavior along eddy peripheries would have provided more useful information on pup behavior when eddies were encountered, but unfortunately because no TDR data were recorded, I could not match diving activity at the temporal and spatial scales needed to detect an association between diving behavior and eddy location.

Additionally, the lack of association of pup locations with either eddy type or region could actually be due to pups not yet knowing to take advantage of these productive regions when they are encountered. Pups had more successful ingestion events when they encountered eddies (Chapter IV), but they did not appear to stay at eddy peripheries, indicating mostly opportunistic foraging behavior during their migration. Pups may not have learned to associate increases in foraging success with eddy peripheries, or they may not have learned to detect current patterns that indicate higher productivity along eddy peripheries. It is also possible that eddies in this area during the winter do not have enhanced prey availability.

True comparisons of the habitat associations of CI and PI pups are not yet possible because a similar habitat association model has not been tested on pups from the PI. Descriptive studies of PI pups do indicate that far fewer individuals reach the

prey-rich TZCF early in their migration. This may prove disadvantageous for those individuals from the PI that do not travel south, and do not encounter regions as prey rich as the TZCF in the north.

Conclusions

Northern fur seal pups from BI showed habitat associations with regions that had high chl a concentrations, were greater distances from shore, had higher SST, and shallower water. Regions of higher chl a concentrations and SST indicate prey rich areas particularly in the TZCF. However, higher SST also have a thermoregulatory benefit for the small pups. Using offshore areas may be an adaptation to avoid predation, but any direct association with bathymetry did not strongly affect habitat choice. The lack of affinity for eddy regions or types indicated that pups were likely naïve about detecting and using productive regions in eddies. Alternatively, eddies in this area and time of year may not have enhanced prey availability. This may have strong implications on pup survival rates if similar behavior is observed in PI pups.

CHAPTER VII

SUMMARY

Conservation of the wide-ranging northern fur seal requires insight into both the worldwide population trends and an examination of specific differences between populations. This study looked at the worldwide northern fur seal population trends and examined the behavior of pups from a stable population on the Commander Islands (CI). The population trends of northern fur seals was modeled to include the effects of migration and revealed that the large Pribilof Islands (PI) population is probably not an important source population for the mostly stable populations present today. However, it was probably an important source population during the first 8 years of repopulating new areas, and the loss of animals from the PI could severely jeopardize the chances of repopulating other areas in the future. The population model also predicted that the quickest population recovery for the PI could be achieved by reducing the mortality rates of both pups and adult females between 10% and 20%.

The high mortality rate of pups at sea makes it particularly crucial to understand differences in pup behavior between stable and unstable, declining populations. The early migratory behavior of CI fur seal pups revealed behavioral similarities with pups from the declining PI, including an increase in the dive depths and dive durations as pups matured during their first winter at sea. Improvements in hunting and diving skills were most likely responsible for the observed changes in pups' early diving behavior. No difference in the maximum dive depths or dive durations was observed, which may

have indicated that pups were constrained by physiological maturity that did not vary by population. Pups from the CI and PI also showed deeper diving during full moon phases, consistent with patterns expected from foraging on vertically migrating fish in the deep scattering layer.

Within three months at sea, individuals began to display one of three diving strategies: shallow daytime diving (shallow divers), deep daytime diving (deep divers), and mixed diving (mixed divers). The shallow diving strategy was the same strategy used by pups from the PI, but the deep diving strategy appeared to be unique to CI pups early in their migration. A recent study by Lea et al (2010) showed some PI pups began conducting deep daytime dives as well, but only after 3 months at sea, whereas pups from the CI started showing deep daytime dives as early as their first month at sea. The occurrence of deep dives throughout the day has also been described in adult females from nearby Medny Island of the CI, indicating some differences in dive behavior between the CI and PI populations.

The use of diving telemetry alone suggested different resource use among individuals with different dive strategies which may have decreased intra-specific competition. However, the stomach temperature data from CI pups showed little differences in actual foraging behavior among all dive strategies. There was no difference in the deepest dive depths of successful ingestion events, nor was there a difference in ingestion event durations among individuals. Daytime foraging behavior was also not unique to deep divers, indicating that shallow divers did occasionally forage during the day. The importance of eddies as foraging habitat for pups was identified,

with over half of successful foraging events occurring at the peripheries of eddies. The high encounter rate of warm-core eddies made them more important as foraging locations compared to cold-core eddies, which were encountered less often. Although pups had high foraging success near eddies, they did not show a strong association with eddies, and pups spent just as much of their time in eddies as they did outside them.

Unfortunately the biggest changes in foraging behavior occurred after two months at sea, at which point most of the deep divers had already stopped transmitting data. If major differences in the foraging success rates or foraging dive depths did occur later in the migratory period, this study was unable to document it. Therefore, the potential advantages of having different dive strategies in the CI population compared to the PI population remains inconclusive and should be investigated further.

The search strategies of CI fur seal pups were compared to those of adult females from the same rookery to determine if similar search strategies were employed. A comparison using the same methods on sea otter foraging behavior over smaller spatio-temporal scales was also conducted, and showed that ARGOS satellite data is inappropriate for some movement pattern indices such as the CRWDiff.

Both CI adult females and pups showed Levy-like search patterns that indicate an efficient foraging search strategy. However, adult females appeared to have a greater preference for travel towards the south-west compared with pups that showed no directional preference when leaving the rookery. The relatively random choice of direction showed by pups indicated little prior knowledge of potentially rich foraging locations, whereas the lactating adult females were likely targeting specific foraging

areas. The spatial scale covered by foraging adult females was approximately 10 times larger than the expected foraging scales of pups (1 km). I suggested that the larger foraging scales indentified in adult females in this study may have been a result of observing two separate, but consecutive foraging bouts, but more likely this was a result of using a movement pattern metric that was inappropriate for the poor resolution ARGOS satellite data.

Finally, a habitat association model was created to identify the most important environmental variables that affected habitat associations. Pups were most likely found in areas with high chlorophyll a concentrations, higher sea surface temperatures and greater distances from shore. Individuals appeared to favor the chlorophyll rich, warm waters of the transition zone chlorophyll front (TZCF) and also preferred the deeper waters of the open ocean compared to following coastlines.

The relatively large proportion of CI pups that travel southwards from their rookery compared to the PI, suggests that the former may reach the prey-rich TZCF earlier in the migratory period. Whether this southward movement is the result of following currents, or from the physical barrier of the Kamchatka peninsula that prevents further westward movement, the results appear to be advantageous to pup survival.

The habitat preferences model did not predict a strong association with either warm-core or cold-core eddies, nor was there a preference for eddy peripheries versus the internal regions of eddies. This observation was contrary to the preference for eddy peripheries, compared to internal regions of eddies or regions outside eddies, observed in juvenile and adult northern fur seals from the PI (Sterling et al. 2009). The use of eddy

peripheries in successful foraging events was identified in pups in this study, but pups also frequently traveled through the centers of eddies which may be why eddy region (i.e., periphery/ internal region) was not a good predictor of habitat choice. It is unknown if PI pups exhibit a similar lack of affinity to eddy peripheries as CI pups.

Pup Survival

As with all other long-lived species, the survival or recovery of a population is highly dependent on survival of the young to reproductive maturity. This study of pups from a stable population provided some information on how behavior could affect survival. Unfortunately, without a long-term, longitudinal study of CI pups, the actual differences in survival rate remain speculative. Potential survival advantages observed from behavioral differences may occur in pups that exhibit the deep diving strategy, as seen in CI pups, and also in the greater proportion of CI pups that reach the prey-rich transition zone early in their migration.

Prior to starting their migration, other factors may affect pup survival. Studies have suggested that nutritional stress may decrease weaning weight and subsequently survival at sea for PI pups. Small pups (less than 14 kg) were found on CI in late October, but we do not know the proportion of this size class that left the rookery, and can only generalize that most CI pups did not appear to be underweight.

The female attendance patterns for CI and PI pups were not compared and are another avenue for future research to assess pup fitness in the two populations. Future research should attempt to quantify pup survival rates from both populations using the

same methods, and over the same study period, to reduce the effects of environmental conditions and prey availability that vary by year. Concurrent monitoring of the pup dive and foraging behavior and long-term survival rates may also provide information on how pups with different behavioral strategies may fare, and consequently, may provide some information on pup survival rates. International cooperation is key to management plans on migratory species that do not recognize political boundaries.

Tale of One

In summer of 2010, one of the pups originally tagged for this study was first observed back on her natal rookery (Fig. 33). No other pups from this study have been observed between 2007 and 2010, despite regular monitoring of the rookery during the summer. The 'missing pups' may have died, moved to a different rookery, or were simply not observed. In addition, this pup was one of the deep diving individuals, which provides some support for the potential advantage of this diving strategy. Unfortunately, such anecdotal information is not enough to base conclusions on what behavioral differences most affect pup survival rates.

The return of this pup serves as a reminder that there is still much to be learned about their natural history during their first migration. Studies such as this one were funded because we have recognized that management practices need to be based on as much information on animal biology and ecology as possible. We have learned a costly lesson by allowing adult females to be killed in the PI based on speculations of

population dynamics. Fortunately, we are given the opportunity to repair the damage we caused, and we are working towards stabilizing the declining population trends.

Fig 33. Three year old pup 74804 returns to Severno-Zapadnoe rookery. Photo: Olga Belonovich.

It is not the first time we have had to manage fur seal populations to allow population growth, but for the first time our efforts are not fueled by the profitability of the fur trade alone. I am hopeful that our good intentions, coupled with continued dedication towards conservation, will eventually result in the recovery of the PI population. I am hopeful not just for future generations or for the maintenance of healthy ecosystems, but also for the sake of all the young seals that take part in these studies. I hope that their contribution towards their species' conservation was not in vain.

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VITA

Name:	Olivia Astillero Lee
Address:	Texas A&M University 200 SeaWolf Parkway, Galveston, TX 77553
Email Address:	olivial@tamu.edu
Education:	B.A. (Honors), Marine Science, University of Hawaii at Hilo, 2004